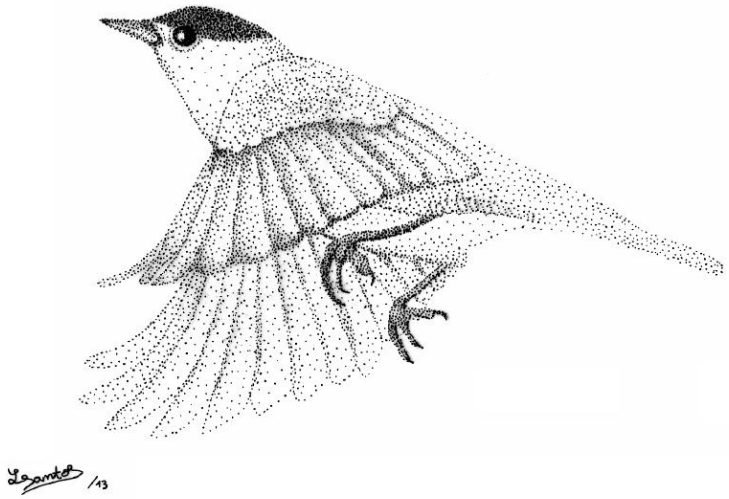

Ecomorphology of sedentary and migratory Blackcap *Sylvia atricapilla* populations in Portuguese continental and island habitats

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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,

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Abstract

The morphology of a given species is determined largely by constraints put on it by the environment and the way the individual uses its habitat. This holds true to the particular demands faced by flying animals, like birds. In these, one of the most important ecological traits shaping morphology are the usually long migratory flights many species, or populations within a species, undertake regularly. However, the requirements for long-distance flight have to be balanced with the species' need to be best adapted to their particular environment, which means that, even within a species, different migratory tendencies results in slightly different morphological traits. Another important factor driving the morphology of many species is the adaptation to the particular characteristics of insular environments, with opposing views arising as to whether size and morphology follow predetermined patterns (the "island rule") or if this general view diminishes the importance of the particular island-species interaction. In the present work we sampled individuals from Blackcap *Sylvia atricapilla* L., 1758 (a passerine model species) from continental Portugal and from the nine islands of the Azores archipelago, in order to assess the differences in morphology of continental migrants and residents, and also the differences of these to sedentary birds from the Azores. These patterns were assessed using both univariate biometric measures and indexes of structural and wing size and shape derived from multivariate principal component analysis. Results confirm most predictions regarding comparisons of sedentary with migratory continental populations, with migrants showing attributes best suited towards maximizing flight efficiency (long, pointed wings), while residents are better adapted towards exploiting their habitat (relatively longer tails, bill and tarsi). The relatively large structural size of migrants when compared to continental sedentary birds is probably best explained by Bergmann's rule. Blackcap populations from the Azores conform in general to island rule predictions, being bigger than continental sedentary birds, falling within the range of migrants. Birds from the more distant Western Group had more pronounced island morphology, with rather large sizes and rounder wings. Some trends associated with distance to mainland and island area are recovered, but are not conclusive.

Keywords: *Sylvia atricapilla*, ecomorphology, migration, island rule, Azores, structural size, wing shape

Resumo

A morfologia de uma espécie é determinada em grande parte por constrangimentos impostos pelo ambiente e pela forma como o indivíduo usa o habitat. Isto é notório face às exigências encontradas por animais voadores, como as aves. Nestas, uma das principais características ecológicas que molda a morfologia são os voos migratórios frequentemente longos que muitas espécies, ou populações dentro da mesma espécie, realizam de forma regular. No entanto, os requisitos para voos de longa distância têm que ser equilibrados com a necessidade de adaptação ao ambiente particular da espécie, o que significa que, mesmo em populações conspecíficas, diferentes tendências migratórias reflectem-se em morfologias ligeiramente diferentes. Outro factor determinante da morfologia de várias espécies é a adaptação às características particulares de ambientes insulares, surgindo versões opostas sobre se o tamanho e a morfologia seguem padrões predeterminados (a "regra insular") ou se esta visão generalista diminui a importância particular da interacção ilha-espécie. No presente trabalho estudamos indivíduos da Toutinegra-de-barrete *Sylvia atricapilla* L., 1758 (uma espécie-modelo de passeriforme) de Portugal continental e das nove ilhas do arquipélago dos Açores, de forma a avaliar diferenças morfológicas entre migradores e sedentários continentais, assim como a diferença destes para aves sedentárias dos Açores. Estes padrões foram analisados com recurso tanto a medidas biométricas univariadas como a índices de tamanho estrutural e forma do corpo e da asa, derivados de análises de componentes principais. Os resultados confirmam a maioria das previsões relativamente à comparação de populações continentais sedentárias e migradoras, as últimas com características para maximizar eficiência em voo (asas longas e agudas), enquanto os sedentários estão melhor adaptados para a exploração do habitat (cauda, bico e tarsos relativamente mais longos). O tamanho estrutural relativamente elevado dos migradores em comparação com os sedentários poderá ser explicado pela regra de Bergmann. Populações de Toutinegra-de-barrete dos Açores estão no geral em conformidade com as previsões da regra insular, sendo maiores que aves continentais sedentárias e incluindo-se na variação dos migradores. Aves do Grupo Ocidental, mais distante, possuem morfologia insular mais pronunciada, com tamanho grande e asas arredondadas. Algumas tendências associadas com a distância ao continente e área da ilha foram encontradas, mas são inconclusivas.

Palavras-chave: *Sylvia atricapilla*, ecomorfologia, migração, regra insular, Açores, tamanho estrutural, forma da asa

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parenthesis are the numbers of individuals of the following three age classes: Adult/Juvenile-First-winter/Unknown. ROM – Paisagem Protegida Regional do Litoral de Vila do Conde e Reserva Ornitológica do Mindelo; PBG – Parque Biológico de Gaia; RNLPT – Reserva Natural Local do Paul de Tornada.

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Abbreviations

CG – Azores Central Group (islands of Terceira, Graciosa, São Jorge, Pico and Faial)

EG – Azores Eastern Group (islands of Santa Maria and São Miguel)

M – Continental migratory birds

PBG – Parque Biológico de Gaia

PCA – Principal component analysis

RNLPT – Reserva Natural Local do Paul de Tornada

ROM – Paisagem Protegida Regional do Litoral de Vila do Conde e Reserva Ornitológica do Mindelo

S – Continental sedentary birds

WG – Azores Western Group (islands of Flores and Corvo)

1 – Introduction

1.1 – Ecomorphology of bird flight

One of the most important factors driving the evolution of animals is the capability of locomotion, which has had a great influence in dispersion and colonization of new areas, favouring allopatric speciation phenomena, the evolution of new feeding habits, escaping predators and adverse environmental conditions, and the evolution of novel reproductive behaviours (Dickinson et al., 2000). Locomotion has evolved independently in many animal taxa in response to different selective pressures, and as such each locomotory style has specific biomechanical requirements (although all locomotory styles conform to the same underlying physical principles, see Dickinson et al., 2000). Thus, morphology has to satisfy these requirements in the best possible way in order to enable the organism to survive and reproduce.

Of the various known locomotion methods, controlled active flight is one the most studied (Hedenstsröm & Spedding, 2008, Dudley & Yanoviak, 2011), and it is used by a great number of species of insects, bats and birds, to which flying becomes an essential survival tool. It has, however, great energetic costs (Hedenström, 1993), as animals which undergo active flight have to counteract both vertical (gravity) and horizontal (drag, due to air friction and wind) forces to prevent the loss of altitude and speed, so they must possess a great range of morphological, physiological and behavioural adaptations capable of optimizing the fitness/cost ratio (Hedenström, 2010).

Given this, birds commonly exhibit a great number of typical morphological and physiological characters aimed at reducing the cost of flight by improving aerodynamic performance (Savile, 1957, Hedenström, 2002), mainly with adaptations in the wing, tail and body morphology to produce lift and reduce drag. While modifications to the external body form act mostly to reduce parasitic drag (drag created by the body isolated from the wings, as the increase of pressure in front of it decelerates air flow) making the body streamlined, and the role of the tail is not yet fully understood (Evans et al., 2002, Hedenström, 2002), the evolution of wings is the most important adaptation to bird flight (Savile, 1957, Lockwood et al., 1998). Bird wings act as airfoils, in which lift is produced both on the underside (positive lift) and upper surface (negative lift) as the wing moves through the air; this movement, however, produces wingtip vortices and associated lift-induced drag, resulting in a loss of lift at the wingtip that can be counteracted by two different mechanisms, slotting the wingtip (by

having the primary feathers forming the wingtip present emarginations on the outer web) or increasing the aspect ratio of the wing (increasing the ratio "wing span^2"/"wing area"), leading to more pointed wings. On the other hand, wings with low aspect ratios are more efficient at low speeds and so are better in conditions when manoeuvrability is important (Savile, 1957, Lockwood et al., 1998).

A good number of studies have tried to establish the relationships between several aspects of bird biology (like migratory behaviour, feeding and reproductive strategies or habitat use) and various parameters of wing morphology, like pointedness (and roundness), convexity (and concavity), wing area and wing loading (Leisler & Thaler, 1982, Lockwood et al., 1998, Pérez-Tris & Tellería, 2001, Peiró, 2003, Fernández & Lank, 2007, Vanhooydonck et al., 2009, de la Hera et al., 2012). Of these parameters, wing pointedness (Fig. 1), which can be defined as the increasing tendency for the wingtip to be defined by the tips of the outermost primaries, is usually the most studied one, as it has been shown to have a direct relationship to high aspect ratio, and to benefit birds in situations when a good speed/energy cost relation is required. Therefore, this is a more common morphological tendency observed in birds that need to undergo long, sustained flight, like migratory birds (Bowlin & Wikelski, 2008), losing benefits associated with manoeuvrability and speed of take-off (better exploited by birds with rounder wings).

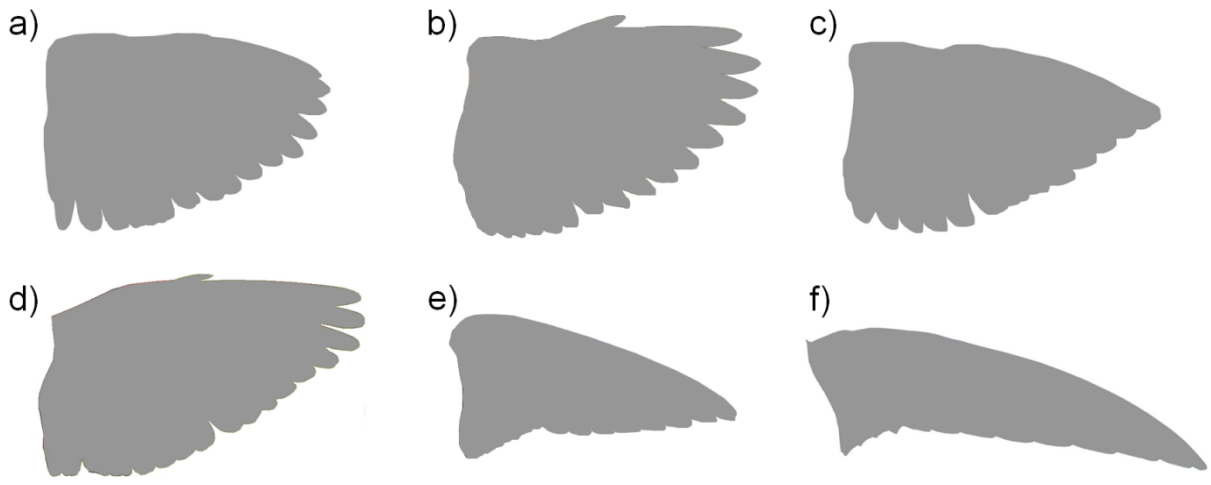

Fig. 1 – Examples of increasing wing shape pointedness in small birds, using the wing outline of a) Dunnock *Prunella modularis*, b) Blackcap *Sylvia atricapilla*, c) Siskin *Carduelis spinus*, d) Wheatear *Oenanthe oenanthe*, e) Sand Martin *Riparia riparia* and f) Swift *Apus apus* (not to scale).

1.2 – Implications of migratory behaviour on morphology

One of the better known aspects of bird ecology, and one that depends on the bird's capacity to fly, is the ability of these animals to migrate, often for great distances. As highly mobile creatures, birds are known to engage in various types of movement, even long distance ones, and a high degree of confusion has arisen in the literature over what kind of movement can be considered as migratory. Here we follow Salewski & Bruderer (2007), who define avian migration as a “regular, endogenously controlled, seasonal movement of birds between breeding and non-breeding areas”. This definition precludes the inclusion of other, irregular, long-distance movements such as irruptions, dispersal and long-distance foraging trips, and we feel its strictness is useful because, apart from corresponding well to the more popular conception of migration, its regular nature will act as a selective pressure that leads to migration-related adaptations to arise. Adaptations for long-distance movement may not be so pronounced in species in which these movements are irregular and have to be weighed against the costs of having the morphology adapted to it (shorter migration distances are well correlated with less pronounced adaptations to long distance flight, see below).

As mentioned before, flight is a costly mode of locomotion, and long-distance migratory flight even more so (Wikelski et al., 2003), hence long-migrant birds are expected to show adaptations (morphological, physiological and behavioural) aimed at minimizing the energy expenditure of forward flight, and this should become more apparent with an increase in migratory distance (Marchetti et al., 1995, Leisler & Winkler, 2003, Baldwin et al., 2010). Therefore, several studies have been developed to understand the general pattern of morphological variation related to migratory behaviour. Winkler & Leisler (1992) surveyed morphological characters from migratory and non-migratory species (both passerines and non-passerines) to find relationships between migratory distance and a wide array of morphological variables, and found out that, as general attributes, migratory birds have wings with higher aspect ratios, less developed hindlimbs and more developed pectoral muscles, with these trends being better appreciated in analysis of passerine morphology, which show less diversity in flight styles, so make for an easier interspecific comparison of flight-related morphology. Among the passerines, they also ran specific analysis on a dataset of 32 morphological characters for 25 species of Sylviidae, finding that an increase in migratory distance correlated well with an increase in several variables, particularly ($p<0.001$) with wing length, aspect ratio, wing pointedness (Kipp's ratio), carpometacarpus length, while the relationship was significantly inverse in regards to tail length and number of notched

primaries; principal component analysis using these 32 characters from sylviids to account for size differences recovered largely the same conclusions. Subsequent inter-specific comparisons focused mostly on wing shape, and have also concluded that migratory behaviour and increasing migratory distances are correlated with increases in wing pointedness (Monkkönen, 1995, Lockwood et al., 1998), wing span (Lockwood et al., 1998, Calmaestra & Moreno, 2001) and aspect ratio (Lockwood et al., 1998, Calmaestra & Moreno, 2001).

While comparing morphology for different species with different migratory behaviour is useful to understand general trends in avian flight apparatus evolution, the results can sometimes be hard to interpret because, apart from concerns regarding different sizes (which can be corrected for with multivariate analysis techniques, see Chandler & Mulvihill, 1988, and Lockwood et al., 1998), differing habitat requirements and flight modes can mask the causes for each species' morphology, so studies have been mostly focused on intra-specific and intra-generic comparisons of populations with different migratory behaviour. It is well know that migratory strategies vary both on inter and intra-specific levels (Pulido, 2007), its plasticity resulting in many cases in populations of the same species that vary between completely migratory long distance travellers and sedentary (resident) populations, and even different strategies within the same population, as different individuals choose between the high demands of migration and staying in unsuitable habitats for wintering or breeding, possibly facing increased competition from conspecifics for limited resources. If there is some stability in the preferred strategy in populations with different behaviour, it's reasonable to expect that small but appreciable differences in morphology should arise.

This is confirmed by the majority of recent studies that have analysed intra-specific or intra-generic differences both between sedentary and migratory populations (Lo Valvo et al., 1988, Mulvihill & Chandler, 1991, Senar et al., 1994, Calmaestra & Moreno, 1998, Tellería & Carbonell, 1999, Pérez-Tris & Tellería, 2001, Egbert & Belthoff, 2003, Fiedler, 2005, Kaboli et al., 2007, Seki et al., 2007, Milá et al., 2008, Outlaw, 2011), or between populations with different distances of migration (Marchetti et al. 1995, Voelker, 2001, Pérez-Tris et al., 2003, Arizaga et al., 2006, Rolshausen et al., 2009, Baldwin et al., 2010, Förschler & Bairlain, 2011, Outlaw, 2011). As with inter-specific analysis, differences have mostly been found in regards to wing shape, with increasing wing pointedness (longer distal primaries) strongly correlated with increasing tendency for long-distance flight in almost every published study (but see below for exceptions), with other associated traits like larger sternum (Calmaestra & Moreno, 1998), shorter hindlimbs (Calmaestra & Moreno, 1998, Tellería & Carbonell, 1999, Milá et al., 2008), shorter tails (Voelker, 2001, Pérez-Tris et al., 2003, Förschler & Bairlein, 2011) and

increasing wing lengths (Lo Valvo et al., 1988, Marchetti et al., 1995, Fitzpatrick, 1998, Tellería & Carbonell, 1999, Pérez-Tris & Tellería, 2001, Voelker, 2001, Pérez-Tris et al., 2003, Fiedler, 2005, Milá et al., 2008, Förschler & Bairlein, 2011, Outlaw, 2011). However, results concerning wing length have been contradictory, with some studies finding no significant differences between some populations with different migratory behaviour (Pérez-Tris & Tellería, 2001, Voelker, 2001, Egbert & Belthoff, 2003), or even sedentary birds with significantly longer wings than migrants (Mulvihill & Chandler, 1991), so some caution is needed when using this criteria as an indication of migratory behaviour. Bill length has been shown to be longer in some migratory populations when compared to residents (Tellería & Carbonell, 1999), but the opposite has also been recovered (Milá et al, 2008).

Sometimes different sex or age categories within a group show different morphology despite similar migratory behaviour: in *Anthus* spp. (Voelker, 2001), increasing wing length in males correlates with migratory distance while the same does not apply to females (although wing shape follows a similar trend); in central-european Bluethroat *Luscinia svecica cyanecula* populations wintering in Spain (Peiró, 1997) adults have more pointed wings than juveniles, and males more pointed wings than females, which is the same pattern observed in Citril Finch *Serinus citrinella* from the West Pyrenees (Alonso & Arizaga, 2006); sedentary Blackcap *Sylvia atricapilla* populations from southern Spain (Pérez-Tris & Tellería, 2001) do not show differences in wing pointedness between adults and juveniles, but for conspecifics wintering in the same spot adults have more pointed wings; in different populations of Yellow-rumped Warbler *Dendroica coronata* (Milá et al., 2008), juveniles tend to have shorter and rounder wings than adults, especially in short or medium-distance migrants. These patterns are to be expected, as inexperienced juveniles are probably at a greater risk of predation than adults during their first year, so better forwards flight performance can be sacrificed for manoeuvrability by means of a more rounded wing. In sedentary birds, forward-flight is not as important a constraint, so adults and juveniles have similar morphology, while for long-distance migrants the high selective pressure for longer wings may override the benefits in manoeuvrability gained by rounder wings. Interestingly, this was not the pattern Peiró (2003) found in Reed Warbler *Acrocephalus scirpaceus* during breeding and post-nuptial migration periods in south-eastern Spain, where juveniles have more pointed wings than adults, although the results could have been influenced by differential feather abrasion on the outermost primaries.

Finally, some studies fail to demonstrate the existence at all of any significant differences in wing shape between migrants and sedentary birds: this was the case in comparisons of migratory and sedentary populations of American Dipper *Cinclus mexicanus*

(Green et al., 2009) and Blackbird *Turdus merula* (Fudickar & Partecke, 2012). These studies, being a minority, also point out factors that could explain why no significant differences in morphology occur: American Dippers undertake low-range (maximum 21 km) altitudinal movements, compared to wide-range latitudinal movements of most European migrants (see Mokwa, 2009 for an example using the Blackcap), with this low-flight range not being enough to override constrains put by the peculiar life style of these birds, and gene flow among sedentary and migratory populations has not been ruled out. Similar hypothesis have been put forward by Fudickar & Partecke (2012) to explain their results.

1.3 – Ecomorphology of island birds

Ever since Darwin (1859) discussed the importance of islands in the process of speciation that island biogeography has been a classic topic in the study of evolution. Islands, especially those located near bigger continents, are usually inhabited by populations or species closely related to mainland groups, but the former usually have different environmental constraints, like small area, different vegetation structure and food resources or the lack of predators that act as selective pressures driving the morphological evolution of these species in different ways to what would happen in the continent's original population. Since many of these situations arose from recent colonizations, and divergence from ancestral mainland populations is still reduced, islands are often privileged locations to study evolutionary processes.

Although each island-mainland-species interaction can be unique and shaped by its own environmental and evolutionary circumstances, it has been noted that the patterns of morphological variation in islands among animal groups follow some predictable tendencies, so much that a general trend, termed the “island rule” (Van Valen, 1973), has been put forward to explain these patterns. This island rule acts as a general graded trend of body size variation, whereas smaller animals have the tendency to become bigger than their mainland counterparts, while the opposite happens with bigger species, converging towards an optimal size for that group of species (see Lomolino, 2005, for a review on vertebrate data). Three main factors could explain this, ecological release, resource limitation and immigrant selection (Fig. 2). In islands species are usually released from size-constraining selective pressures acting on more high-competition and species-rich habitats in the mainland, like predation, parasitism, mutualism or competition (this reduction in interspecific selective pressures is termed ecological release). On the other hand, in islands it is usual to encounter high population densities, which could lead to higher intraspecific competition for limited

resources. Resource limitation occurs mostly in smaller islands, and could promote both dwarfism (smaller individuals require less energy) and gigantism (larger sizes are beneficial in intraspecific disputes). Immigrant selection acts mostly on smaller animals to promote gigantism, by selecting for the more vagile individuals (larger individuals tend to disperse more easily and to further away). The effects of immigrant selection are expected to be more pronounced early in the colonization (as later the constrains put on by ecological release and resource limitation may be stronger) and in the more distant islands.

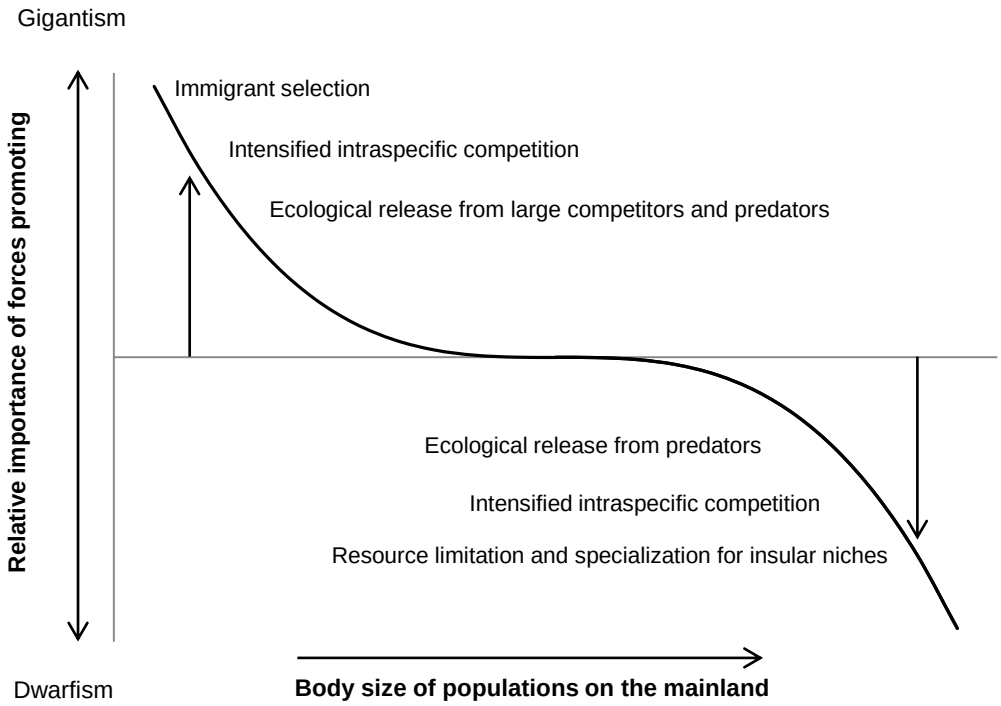

Fig. 2 – Proposed model of selective pressures acting on the body size of insular animals, promoting gigantism in smaller species and dwarfism in larger species, according to the "island rule" (Lomolino, 2005). The increase in size of smaller species can be explained by increased dispersal ability of larger individuals (immigrant selection), reduced interspecific competition and predation from larger animals, while intensified intraspecific competition may drive increases in body size that benefit individuals in confrontations with conspecifics. For larger species, the release from predation means large body sizes are no longer needed for protection, while limiting resources push for smaller sizes in order to reduce energy consumption and optimize resource sharing. Adapted from Lomolino (2005).

Despite a large body of work pointing to some degree towards predictable patterns of body size change in island populations, recent studies (Meiri et al., 2006, Meiri et al., 2008, McClain et al., 2013) have found limited or no support for their occurrence. The authors argue that trends are clade-specific, not size-specific, and depend on ecological factors, the species' biology and the ecological and historical context in which the colonization took place. McNab (2002), while conceding the generality of the application of the island rule,

highlighted the need to look at resource availability and sharing as factors determining vertebrate insular body size. This author also cited earlier studies that suggest that resource limitation on islands may lead to an increase in tolerance to conspecifics, instead of increased competition.

Birds are an ideal study group to test predictions related to insular evolution, as they are highly mobile and thus more easily colonize island habitats than other taxa, so much work has been done to understand ecological, morphological and behavioural aspects of bird island colonization (Blondel, 2000). Studies on multiple-taxa bird morphological databases, focusing on terrestrial birds (as marine or highly aerial taxa are probably not susceptible to the island environment in the same way) lend some support to the aforementioned island rule. Clegg & Owens (2002) analysed trends in size change using body mass and bill-to-skull length using diverse literature data from mainland-island systems, their results suggesting that the island rule should be upheld as a general pattern in birds for both morphological variables tested: overall body size increased in small-bodied forms and decreased in larger taxa; bill lengths also roughly converged towards an optimal bill size, that could be used to exploit a bigger variety of food resources. These authors hypothesize that these changes could be brought about by increased competition in the restricted island habitat, a similar idea to the resource limitation hypothesis advanced by Lomolino (2005). In a study on Pacific island birds, Boyer & Jetz (2010) gathered information from the fossil record and modern bird distribution data to match morphological correlates of size (hindlimb skeletal measures) with physical attributes of island size (land area, maximum elevation and distance from mainland). Although they found a relationship between increasing body size in island birds and increase in land area and decrease in distance to continents, the results suggest that simple island rule-like explanations may be simplistic and several evolutionary and ecological factors should be considered in further studies. In another study, Fitzpatrick (1998) compared the size (wing length used as a proxy) of sedentary, migratory and insular populations in a wide range of European species (mostly terrestrial, but also some marine species), and found that as a general rule migration imposes a constraint towards longer wings and island residency an opposite effect, such that continental migrants tend to have longer wings than continental residents, who in turn have longer wings than insular populations.

Similarly to ecomorphological studies mentioned before on migratory versus sedentary traits, many studies have been centred on the comparison between continental and insular populations of the same species or group of species, and likewise these cases show that slight but appreciable differences occur in these populations as a reflection of the peculiar ecoevolutionary characteristics of island habitats. However, contrary to the generally

predictable patterns found in migratory vs. sedentary morphological comparisons, often contradictory trends have been shown by many studies regarding many morphological variables in island populations: shorter wings (Grant, 1979, Alonso et al., 2006, Förschler et al., 2007, Förschler et al., 2008) or longer wings (Clegg et al., 2008, Wright & Steadman, 2012); lower body mass (Blondel et al., 2006), higher body mass (Grant, 1979, Clegg et al., 2008, Mathys & Lockwood, 2009) or similar (Carrascal et al., 1994, Wright & Steadman, 2012); larger hindleg elements (Grant, 1979, Carrascal et al., 1994, Komdeur et al., 2004, Wright & Steadman, 2012) or smaller hindleg elements (Blondel et al., 2006, Förschler et al., 2007). The most coherent patterns have been found regarding wing shape, with island birds having more rounded wings (Förschler et al., 2007, Förschler et al., 2008, but see Komdeur et al., 2004 for an exception) and bill size, with island birds usually with bigger beaks (Grant, 1979, Scott et al., 2003, Förschler et al., 2007, Clegg et al., 2008, Mathys & Lockwood, 2009, Wright & Steadman, 2012), presumably to take advantage of a bigger array of feeding possibilities in the face of decreased interspecific competition compared to the mainland. All of this gives further indication that simple generalizations may be inadequate when discussing the effect of insularity on morphological evolution, and more attention should be given to the specific organism-island system under study.

1.4 – Migratory patterns and migratory ecomorphology in the Blackcap

The Blackcap *Sylvia atricapilla* L., 1758 (Fig. 3) is one of the most abundant and cosmopolitan passerines in the Western Palearctic, preferring mostly forests and other habitats where shrubs are present (Cramp & Brooks, 1992). Its large geographic range, coupled with a complex array of migratory patterns, has led to the recognition of five subspecies that differ slightly in their morphology, coloration and geographic occurrence (Vaurie, 1954, Cramp & Brooks, 1992): *S. a. atricapilla* L., 1758, from most continental Europe to western Siberia; *S. a. dammholzi* Stresemann, 1928, from Eastern Europe and the Middle East; *S. a. pauluccii* Arrigoni, 1902, from Corsica, Sardinia, Balearic Islands, Tunisia and south and central continental Italy; *S. a. heineken* Jardine, 1830, from Madeira, Canary Islands and the West and Southwest of the Iberian peninsula (possibly also North Africa); *S. a. gularis* Alexander, 1898, from the Azores and Cape Verde. These races combine a wide range of migratory strategies, from completely sedentary birds to long distance migrants (Berthold & Helbig, 1992, Pérez-Tris et al., 2004, Fiedler, 2005). Therefore, Blackcap has been one of the model species used for approaching a wide array of bird migration questions. Studies on morphology, physiology, phenology, differential migration, orientation

and the genetic control of migration have been focused on this species (Berthold et al., 2003).

Fig. 3 – Blackcap *Sylvia atricapilla* L., 1758. Male (on the front) and female (Marcos Oliveira).

As migration usually arises to take advantage of the best environmental conditions in highly seasonal places like temperate zones (Salewski & Bruderer, 2007), in most species' populations a gradient of increasing migratory behaviour and morphology is found from lower to higher latitudes, and that is very well exemplified in the Blackcap. Fiedler (2005) compared Blackcap populations from 8 different locations in Europe and Macaronesia, from the subspecies *S. a. gularis*, *S. a. heineken*, *S. a. paulucci* and *S. a. atricapilla* (with some of the included populations probably belonging to *S. a. dammholzi*) regarding migratory related morphological characters and found that from southern to northern populations there is an increase in wing length, pointedness, aspect ratio and area, and decrease in wing loading, the expected pattern if an increase in migratory tendency occurs in Northern populations. There is also a gradual increase in size (body mass was used as a proxy) towards Northern populations, which is also expected according to Bergmann's rule (an ecogeographical rule that states that, within taxa, populations from colder environments, usually from higher latitudes, tend to have a larger body size when compared to populations from warmer environments). Comparisons with island birds in the same study didn't reveal such a clear cut pattern. We will refer to this subject later in this introduction. Similarly, studies on ringing recoveries (Mokwa, 2009) also suggest this pattern, with North European populations highly migratory, in the northern range completely vacating breeding quarters during the autumn migration period, and some South European populations completely sedentary throughout

the year (although a good number of birds is known to exhibit northward migratory tendencies in autumn, see Fransson & Stolt, 1993 and Bengtsson et al., 2009). There is some evidence to suggest that female Blackcaps could move longer distances to the South for wintering, but nothing conclusive could be determined (Catry et al., 2006).

In Iberia, populations of the subspecies *S. a. atricapilla* and *S. a. heineken* occur regularly, the first as Central and Northwest European migrants and North Iberian residents or migrants, and the latter as residents in the southern part of Iberia (Cramp & Brooks, 1992). Ringing recoveries show that the vast majority of migrants come from Western Europe, and suggest that the majority of migrants in Iberia use the peninsula as a migratory pathway but not as a final wintering site (Cantos, 1995). This pattern supports evidence from wider European studies on ringing recoveries (Fransson, 1995), genetic markers (Pérez-Tris et al., 2004, Rolshausen et al., 2009) and orientation experiments (Busse, 2001, Ozarowska et al., 2004) of the occurrence of a migratory divide among North European Blackcap populations that separates individuals that fly through Southeast Europe and others that fly through Southwest Europe in the Autumn migration. The main periods of migration in Iberia are between February-March and September-November (Cantos, 1995, Grandio, 1997, Catry et al., 2010). Arizaga & Barba (2009), studying differential migration of Blackcaps passing through a shrubby area near the Pyrenees, found that during Autumn migration there is no differential passage between sexes, but it occurs among age classes (juveniles first), while during Spring migration there is differential passage among sex (males first) and age classes (adults first). But other studies (Cantos, 1995, Leal et al., 2004) have not found such patterns (probably due to improper sampling).

Although the morphological differences between migratory and sedentary Iberian Blackcaps are smaller than those observed when they are compared to North European populations (Fiedler, 2005), evidence suggests they are nevertheless significant and important. Probably the most complete work on the morphology of Iberian blackcaps has been done by Tellería & Carbonell (1999), who studied five different populations from the peninsula across a North-South axis, with ringing recoveries suggesting also a gradient of decreasing migratory behaviour from completely migratory northern highland populations to completely sedentary lowland populations. Analysing various morphometric characters, they conclude that this migratory gradient reflects also a morphological gradient in which, as we move towards southern populations that are increasingly sedentary, wing length and wing pointedness tend to decrease, while body weight, structural size and the length of tail, bill and tarsus tend to increase, possibly reflecting also different abundance of food sources during individual growth or different habitat use. These conclusions have been used in

subsequent studies (Pérez-Tris et al., 1999, de la Hera et al., 2007) to build discriminant functions to classify Iberian populations as migratory or sedentary according to a specific set of characters. These results have contradicted some conclusions of a previous study by Finlayson (1981), who studied Blackcap populations from Gibraltar (one of the southern areas sampled by Tellería & Carbonell (1999)) and recovered a pattern of shorter wings, lower body weight and similar tarsus and bill length in resident birds (*S. a. heineken*) compared to presumed wintering birds of the nominate subspecies. However, this older study does not explain clearly how separation of birds from the two populations was made, so it is possible that some birds could have been misclassified given that all studied individuals were trapped during the winter, when there is a mixture of migratory and sedentary birds.

1.5 – Adaptations to island ecosystems in the Blackcap

As well as being one of the most common bird species in the Western Palearctic in forest habitat, the Blackcap is also one of the predominant forest passerines in the volcanic islands that form the Macaronesia (Madeira, Canary Islands, Cape Verde and the Azores), where two subspecies are traditionally considered to occur, *S. atricapilla heineken* in Madeira and the Canary Islands, and *S. atricapilla gularis* in Cape Verde and the Azores (Cramp & Brooks, 1992). Recent evidence from genetic markers (Pérez-Tris et al., 2004, Dietzen et al., 2008), however, seems to contradict the traditional morphological-based distinction of these subspecies, showing that there is little to differentiate continental from island populations conclusively, with Atlantic populations closely linked to western continental migratory populations, with morphology too variable for any conclusive assertion. A recent work focusing on birds from the Azores archipelago (Rodrigues, 2012) also reveals relatively little genetic differentiation between populations from these islands and Madeira and the mainland, indicating that either of these two areas could be the place of origin of Azorean Blackcaps (possibly via a single colonization event), with the distant Cape Verde islands not a good candidate (however, these populations were not analysed), indicating as well the possibility of gene flow occurring among the Azores islands. The same study also analysed univariate measures of morphology of Blackcaps from all nine islands of the archipelago, revealing, like Dietzen et al. (2008), high variability among and within islands, with birds from the more distant Western Group islands (Flores and Corvo) being on average bigger.

If insular Blackcap conforms to the “island-rule” and non-migratory morphology predictions, we should expect that comparisons between Macaronesia Blackcap and continental birds should reveal individuals on average as being bigger and with rounder,

shorter wings. This simple pattern, however, has not been recovered in a comparison of the morphology of Blackcap from several European and Atlantic island populations (Fiedler, 2005). In this study, data on Macaronesia birds was analysed for Madeira (representing *S. a. heineken*) and Cape Verde (representing *S. a. gularis*) mostly from wing morphological characters, along with body mass. Using this variable as a proxy of body size, Madeira birds were the smallest of all the populations under study, with Cape Verde birds only smaller than North European populations, and a similar pattern was found regarding wing length. The analysis of wing shape recovered a different pattern, with birds from Cape Verde similar to Mediterranean birds having very rounded wings, and birds from Madeira showing scores of the wing shape index and aspect ratio in the range of Central European populations. Although birds from Cape Verde were used in this study to represent the *S. a. gularis* group, that traditionally includes birds from the Azores, caution should be taken when generalizing these results to birds from the Portuguese archipelago, as genetic evidence suggests these populations may not be so closely related (see above). In a study on insular versus continental wing length in a wide sample of European bird species (Fitzpatrick, 1998), continental residents had in general longer wings than island subspecies, but in the Blackcap the opposite to the general trend was verified. In this study, *S. a. gularis* individuals had on average longer wings than continental sedentary *S. a. heineken*.

These results from studies on Blackcap island populations further demonstrate that simple generalizations are insufficient to explain the morphology of island birds, and case-specific studies should be undertaken before trying to explain the morphological characters of these birds.

1.6 – Objectives

The main objective of this work is to analyse and compare the ecomorphology of Blackcap *Sylvia atricapilla* populations from the Portuguese mainland and the Portuguese archipelago of the Azores, in order to assess the occurrence of patterns of morphological variation usually attributed to island birds. As birds from continental sites include sedentary birds and migrants with a mostly West-European provenance, the classification and comparison of migration-related morphological characters between continental birds and putative sedentary island birds will also be undertaken, as well as finer inter-island group comparisons.

2 – Methods

2.1 – Sampling sites

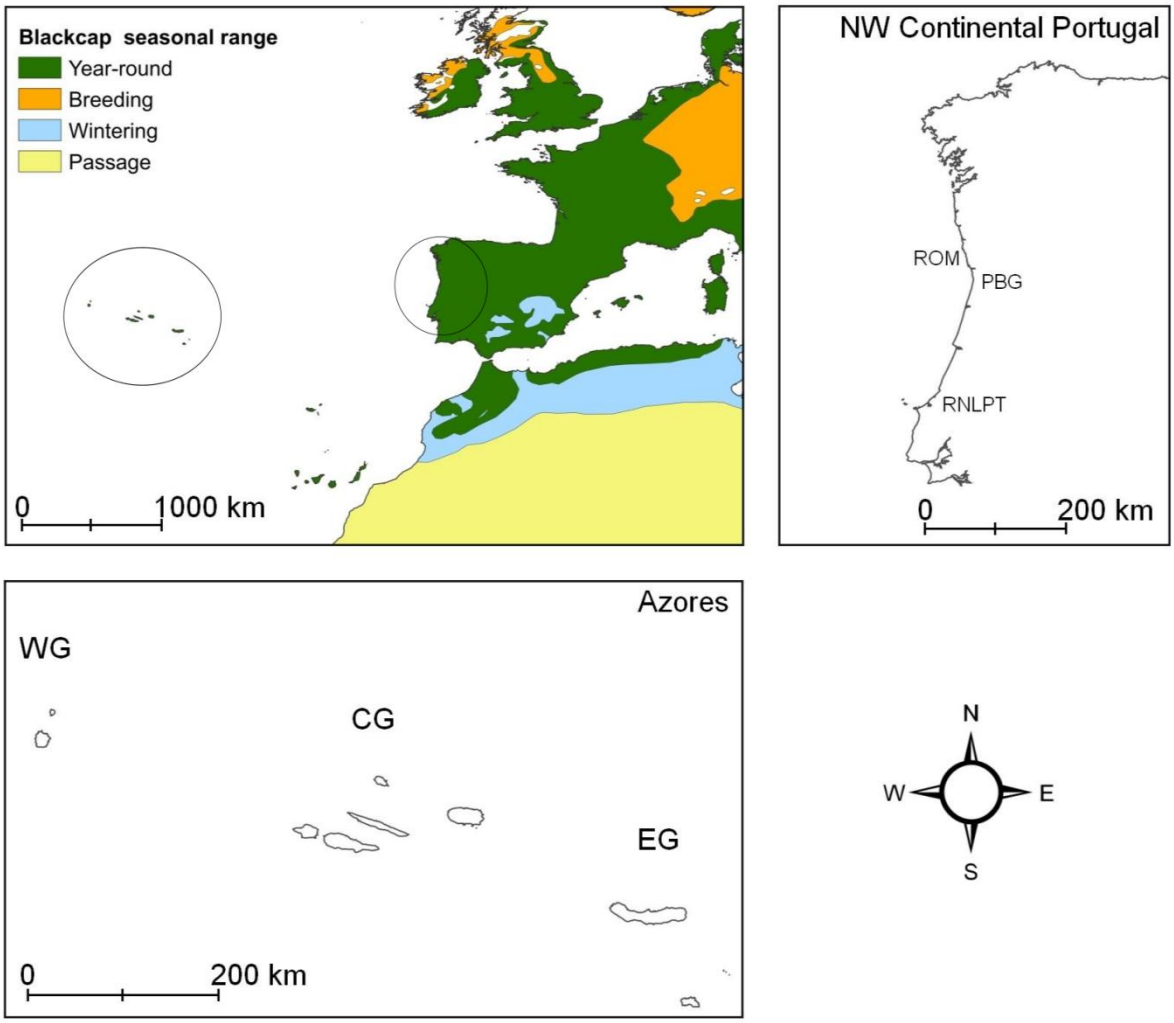

Fig. 4 – Geographic placement of continental Portugal and the Azores archipelago in Southwestern Europe, with information on the phenology of Blackcap populations in this region. The three sampling sites in continental Portugal are: Paisagem Protegida Regional do Litoral de Vila do Conde e Reserva Ornitológica do Mindelo (ROM), Parque Biológico de Gaia (PBG) and Reserva Natural Local do Paul de Tornada (RNLPT). The Azores archipelago is composed of three main groups of islands, the Eastern Group (EG), the Central Group (CG) and the Western Group (WG), each successively further away from the European continent. Sampling was done on all nine islands: Santa Maria and São Miguel (EG); Terceira, Graciosa, São Jorge, Pico and Faial (CG); Corvo and Flores (WG). Maps were obtained from BirdLife International & NatureServe (2011) and Instituto Hidrográfico da Marinha.

Paisagem Protegida Regional do Litoral de Vila do Conde e Reserva Ornitológica do Mindelo (ROM): ROM is a small local protected area (380 ha) in the North coast of continental Portugal (Mindelo, Vila do Conde, Porto, 41°19′23″N, 8°43′52″W), with a mixture of sand dunes, agricultural and open forest habitats. Sampling took place in May of 2013 in

the latter habitats, in areas of mixed forests of *Pinus pinaster*, *Quercus robur*, *Eucalyptus globulus*, *Acacia longifolia* and *Salix atrocinerea*, with well-developed undergrowth (mostly *Rubus* sp. and *Oenanthe crocata*).

Parque Biológico de Gaia (PBG): PBG is a 35 ha urban park in the North of mainland Portugal (Avintes, Vila Nova de Gaia, Porto, 41°05'48.50"N, 8°33'21.34"W) with plant communities dominated mostly by autochthonous deciduous tree species, with dispersed heath, broom and gorse-dominated areas, *Pinus pinaster* and *Acacia longifolia* forests and small agricultural areas. Data collection in PBG was irregular between February and May of 2013, mostly focused on the pre-breeding migration season (February). Additional records for some morphological variables were taken from a pre-existing database with data from 2009 to 2011. Sampling took place in forest areas close to a river with well-developed undergrowth (dominated by *Rubus* sp., *Sambucus nigra* and *Hedera helix*) and tree communities (dominated by *Quercus robur*, *Alnus glutinosa*, *Salix atrocinerea* and *Acacia longifolia*).

Reserva Natural Local do Paul de Tornada (RNLPT): the area of the RNLPT in Central mainland Portugal (Tornada, Caldas da Rainha, Leiria, 39°26'53.38"N, 9°07'51.67"W) is mostly made up of a permanent *Phragmites australis* reed bed (25 ha), with the remaining area (20 ha) made up of a mosaic of small riparian corridors (dominated by *Salix atrocinerea*, *Rubus* sp., *Phragmites australis* and *Arundo donax*), shrubland (*Rubus* sp., *Arundo donax*, *Crataegus monogyna* and *Cydonia oblonga*) and grassland areas. Data collection was done regulary at the RNLPT from the 15th of September to the 29th of November of 2012, during the main post-breeding migratory period of *S. atricapilla*, in the marginal habitats (riparian corridor and shrubland).

Azores: The Azores is a nine-island archipelago in the Atlantic Ocean, usually considered geographically in 3 main groups: the Eastern Group (Santa Maria and São Miguel), the Central Group (Terceira, Graciosa, Faial, Pico and São Jorge) and the Western Group (Flores and Corvo). The archipelago has an approximate range of 36°44–39°43'N, 24°45–31°17' W. Several locations in all of the islands were sampled. In São Miguel birds were collected near the Sete Cidades and Furnas lakes, in production forests with *Cryptomeria japonica* and *Pittosporum undulatum*, and also in Tronqueira (in the east part of the island), in the middle of a native forest with *Laurus azorica*, *Erica azorica* and *Myrica faya*. In Graciosa and Corvo all the birds were collected on valleys with forests surrounded by

pasture fields (predominant plant species include *Laurus azorica*, *Erica azorica*, *Cryptomeria japonica* and *Pittosporum undulatum*). In all other islands, birds were collected around the entire island, in native forests (*Juniperus brevifolia*, *Erica azorica* and *Laurus azorica*) and in production forests with *Cryptomeria japonica* and *Pittosporum undulatum* in the edge of pasture fields.

2.2 – Biometric data collection

Bird data collection involved the capture of live bird specimens with the use of mist nets at the locations mentioned above. All birds captured were fitted with a unique numbered ring (or if they already had one the ring number was recorded, to prevent duplicate results), sexed and aged (Svensson, 1992, Jenni & Winkler, 1994). Since Blackcaps are known to undergo a partial post-juvenile moult, all juvenile (captured before moult) and first-winter birds (captured after moult) were grouped in the same age class, "Juvenile/1st-Winter", as they retain the same set of primary feathers. Individuals captured after their first post-nuptial moult were grouped together as "Adult" birds. Afterwards, a series of biometrical measures were recorded (measurements follow Svensson (1992), unless otherwise noted). These were weight (with a 0.1 g precision), beak length (with a 0.1 mm precision), tarsus length (with a 0.1 mm precision), tail length (with a 0.5 mm precision), wing length (maximum wing chord, with a 0.5 mm precision) and length of primaries 1 to 9 (with a 0.5 mm precision), numbered descendantly and excluding the outermost vestigial primary. The recording of the wing formula was done in two ways, either as the length of each feather from the carpal joint with a stopped-ruler (P1, P2... P9, Svensson, 1992) or as the length of each feather measured with a pin-ruler on its outer web until the point where it enters the skin, except for primary 9 which was measured on the inner web (P1P, P2P... P9P, Jenni & Winkler, 1989). No measurements were taken on feathers that were heavily worn or growing, and all wing measurements were taken on the bird's right wing. Birds that showed signs of stress were also released without measuring. All measurements on birds from ROM, PBG and RNLPT were taken by P. Andrade. Measurements from birds from the Azores were gently provided by Pedro Rodrigues (CIBIO-Açores).

2.3 – Data analysis

Data analysis for the present work was carried out using the software package STATISTICA v.11 (StatSoft, Inc., 2012).

Data standardization: Comparison of morphological data from different sources, especially when variables were measured in different ways, is a less than ideal situation in ecomorphological studies. However, this was a necessity during the elaboration of the present study, as data from the Azores was only available after most data collection on the continent had occurred, so data standardization procedures were undertaken to ensure that valid conclusions could be achieved.

Wing feather lengths of birds from the continent were measured from the carpal joint on a flattened wing (Svenson, 1992), while for birds from the Azores this measurement was taken with a pin-ruler on the outer web of each feather (according to Jenni & Winkler, 1989). To create a comparison group for these variables, a subset of birds from PBG and ROM was measured using both wing formula measurements. Simple linear regressions were done on all stopped-ruler/pin-ruler feather pairs to check for the best correlations (Pearson's correlation), for which regression equations were recovered. These were afterwards used to predict missing values to obtain wing formula measurements.

Bill length measurements were done according to Svenson (1992, "normal bill length") except for the birds captured at RNLPT, in which the bill length measurement was done according to Redfern & Clark (2001), with the callipers placed horizontally (herein termed "alternative bill length"). Since most birds from PBG and all from ROM were measured in both ways, data from these was used to conduct a simple linear regression, and the regression equation that was obtained was then used to predict normal bill length values for birds from RNLPT.

Wing shape: From simple indices to more complex multivariate approaches, many ways have been proposed to quantify the shape of the wing, mainly its pointedness (Lockwood et al., 1998). Even though most of them are useful in representing the shape of the external flight apparatus of the bird, multivariate approaches, like principal component analysis (PCA, Chandler & Mulvihill, 1988) and size-constrained component analysis (SCCA, Lockwood et al., 1998) have been increasingly used in recent studies of wing shape as they are able to account for all the dimensions of the variables (wing feather lengths, in this case), and reduce them to a number of orthogonal principal components. For example, most studies recover the first component (PC1) as a component of size, a second component (PC2) representing wing pointedness and a third (PC3) usually representing wing convexity (Lockwood et al., 1998). For the analysis of the wing shape of continental and insular Blackcaps, a PCA analysis using the length of each primary feather was conducted to assess wing shape (using the stopped-ruler method). This was also done using the C2 index

presented by Lockwood et al. (1998), which is an index of wing roundness (the results were multiplied by -1 to represent pointedness in a more intuitive manner).

Apart from the results derived from multivariate techniques, simpler indices have also been proposed to represent the shape of the wing, and although they cannot compensate for the effects of allometry as effectively as multivariate techniques, they can nonetheless be used with good confidence to quantify wing pointedness (Lockwood et al., 1998). The following indices were thus applied for comparison, using simple linear regressions (see Tab. 1 for a review of these indices): Hendenström's P5 and P9 indices (Hedenström & Pettersson, 1986), the P1-P9 index (Pérez-Tris et al., 1999) and a modification of Kipp's index (Lockwood et al., 1998, using the innermost primary instead of the outermost secondary feather). The modification to Kipp's index means the results should not be compared to the results on other studies, but they nonetheless maintain their consistency within the framework of the present work.

Tab. 1 – Wing shape indices used in this study. WS, wing shape; WL, wing length; Px, length of primary feather x measured with a stopped-ruler; PxP, length of primary feather x measured with a pin-ruler; ΔPx, distance of primary x to wingtip.

Index	Formula	Reference
C2 (-)	$-\ln(3.332\,P9P^{-3.490}P8P^{-1.816}P7P^{-0.893}P6P^{-0.003}P5P^{0.829}P4P^{1.351}P3P^{1.661}P2P^{2.363})$	Modified from Lockwood et al. (1998)
Hedenström's P9	$100(\frac{WL-\Delta P9}{WL})$	Hedenström & Pettersson (1986)
Hendeström's P5	$100(\frac{WL-\Delta P5}{WL})$	Hedenström & Pettersson (1986)
P1-P9	$(P7-P1)-(P7-P9)$	Pérez-Tris et al. (1999)
Kipp's (modified)	$100(\frac{\Delta P1}{WL})$	Modified from Lockwood et al. (1998)

Structural size and shape: despite being one of the most important determinants of an animal's biology, body size has traditionally been rather hard to measure and analyse in a biological meaningful way. In birds, many different morphological variables have been proposed as proxies of body size, mostly wing length and body mass, but these can be unreliable due to individual or season variation (Rising & Somers, 1989). Other morphometric variables, like tarsus and keel lengths (Senar & Pascual, 1997) have been found to correlate well with body size or structural size (considered as the first principal component of a PCA with skeletal measurements), but like mentioned previously in regards to wing shape, the best way to take into account the effects of a large number of variables is to undergo a PCA (Rising & Somers, 1989). Besides body size, variation in body shape is also analysed (using

other components of the PCA). For this study we used the length of the wing, tail, beak and tarsus as variables in a PCA.

Migratory strategy classification: Although a wide array of studies demonstrates that as a general rule migrants display some characteristic morphological tendencies when compared to con-specific sedentary populations, the occurrence of individual variation on any given morphological variable (such as wing length, or wing pointedness) usually attributable to the effect of migratory behaviour in a population makes it very difficult to use single characters to classify a given individual as a migrant or as a sedentary bird. This can be done if the bird's population of origin can be well established (for example, in populations with high degree of morphological differentiation), but in cases like the Blackcap, where there are few morphological differences in populations across Europe when a migratory gradient is taken into consideration, other strategies have to be employed. Pérez-Tris et al. (1999) used morphological traits relevant to migratory flight performance (wing length, wing shape and tail length) to create a discriminant function that could accurately classify Iberian sedentary and migratory populations. For this they used birds captured at five different localities in Spain across a North-South axis, in which Blackcaps from the North are known to vacate breeding areasto winter in the southern localities, where completely sedentary populations can be found (Tellería & Carbonell, 1999). This model proved very accurate in classifying birds regarding their migratory behaviour (91.78% and 87.41% of migratory and sedentary Blackcaps correctly classified, respectively), with the most visible limitation the probability of underestimating the true number of sedentary individuals in the population. This discriminant function analysis was further improved by de la Hera et al. (2007), who used a higher number of birds captured at three of the five sites used by Pérez-Tris et al. (1999) to develop new classification functions, the usefulness of which was corroborated using posterior classification probability analysis. This model (de la Hera et al., 2007) is used in the present study to classify Blackcaps as either migratory or sedentary, and consists of two classification functions that are applied to each individual bird:

$$M = -719.13 + 6.05*T + 19.92*P8P – 2.98*WS$$
$$S = -703.20 + 6.95*T + 18.73*P8P – 4.01*WS$$

in which T is tail length (mm), P8P is the length of the eighth primary feather measured with a pin-ruler to the point where it enters the skin (mm) and WS is the wing shape index P1-P9. Birds are classified into the group whose function they had the higher

classification score.

Continent-island morphological comparison: In order to assess differences in morphology between birds from continental Portugal and the Azores we grouped individuals in five classes according to their place of origin and migratory behaviour (de la Hera et al., 2007). These classes are: 1) continental migrants; 2) continental sedentary; 3) Eastern Group; 4) Central Group; and 5) Western Group. Four univariate measures (lengths of wing, tail, bill and tarsus) and multivariate indices of wing and body size and shape (derived from the previous PCAs) were used for this comparison. Since none of these showed a normal distribution (even after performing a Box-Cox transformation), we conducted a non-parametric analysis of variance (Kruskal-Wallis *H*-test) to check for significant differences in the morphology between the 5 classes, followed by a post-hoc multiple comparison of ranks test (Dunn's test) to identify pairs of groups with significant differences for each variable.

To assess the effect of island characteristics and morphology in our Azorean Blackcap sample, simple linear regressions were done to see the relationships between multivariate indices of wing and structural size and shape with two important descriptors of island physical geography (Tab. 2), island area (km^2) and approximate distance to the nearest continent (km).

Tab. 2 – Area (km^2) and distance to mainland (km) for the five islands of the Azores (approximate values). Values taken from Cardoso et al. (2010).

Geographical group	Island	Area (km^2)	Distance to mainland (km)
Eastern Group	Santa Maria	97	1343
	São Miguel	750	1358
Central Group	Terceira	400	1552
	São Jorge	246	1614
	Graciosa	62	1625
	Pico	436	1640
	Faial	173	1688
Western Group	Corvo	17	1890
	Flores	143	1898

3 – Results

Fieldwork in the 12 study sites (three from continental Portugal and the nine islands of the Azores) resulted in the collection of data from a total of 411 birds (Tab. 3). Of these, 233 individuals were captured in the three continental sites and 178 in the Azores. Apart from 5 juvenile individuals captured at PBG and RNLPT that had not yet underwent the post-juvenile moult, 406 individuals could be sexed. Of these, 224 (55.17%) were males and 182 (44.83%) were females. 72 birds were classified as adults and 222 as juveniles, plus 117 birds for which the correct age could not be determined.

Tab. 3 – Summary of captures in each study location by sex and age (adult, juvenile/first-winter and undetermined) classes. ROM – Paisagem Protegida Regional do Litoral de Vila do Conde e Reserva Ornitológica do Mindelo; PBG – Parque Biológico de Gaia; RNLPT – Reserva Natural Local do Paul de Tornada.

			Male			Female			Unknown	**Total**
			Adult	Juv./1st W.	Un.	Adult	Juv./1st W.	Un.	Juv.	
Continental Portugal		*ROM*	1	-	1	1	3	2	-	8
		PBG	27	50	9	22	33	2	2	145
		RNLPT	6	33	12	6	28	2	3	80
Azores	*Eastern Group*	*Santa Maria*	-	6	3	-	5	6	-	33
		São Miguel	-	11	1	1	4	5	-	28
	Central Group	*Terceira*	-	5	2	1	2	5	-	19
		Graciosa	5	2	2	1	4	5	-	29
		São Jorge	-	1	5	-	4	4	-	12
		Pico	-	4		-	4	2	-	11
		Faial	-	3		-	5	3	-	13
	Western Group	*Flores*	-	4		-	4	11	-	21
		Corvo	-	-		1	2	4	-	12
		Total	39	119	66	33	98	51	5	**411**

3.1 – Data standardization

Since wing feather measurements of birds from the Azores were only done with the pin-ruler method (PxP, Jenni & Winkler, 1989), and birds from the continent were measured primarily with the stopped-ruler method (Px, Svensson, 1992), predictive equations for all of

these values were obtained using simple linear regression analysis based on a subset of birds from ROM and PBG (Tab. 4). All stopped-ruler/pin-ruler pairs were significantly correlated ($p<0.05$), most of them highly significantly ($p<0.001$). For the majority of cases, the best predictor was the measure of the same feather using the different measuring technique. In addition, this analysis was also carried out to compare measures of bill length, which were also significantly correlated ($n=55$, $r=0.751$, $p<0.05$), with the resulting regression equation used to predict values of "normal" bill length in birds from RNLPT from "alternative" bill length values.

Tab. 4 – Summary of simple linear regression analysis used to predict stopped-ruler values of wing primary feather length (Px) using pin-ruler measurements (PxP), and vice versa. Sample size (n), Pearson's correlation coefficients (r) and regression line equations for each correlation are shown.

Primary length	Predictor	n	r	Predictive equation
P1P	P2	31	0.765***	13.731+0.58210*P2
P2P	P2	32	0.845***	5.3935+0.74444*P2
P3P	P2	32	0.792***	14.618+0.59785*P2
P4P	P4	32	0.809***	6.2904+0.70483*P4
P5P	P5	31	0.853***	-2.275+0.82528*P5
P6P	P6	31	0.856***	3.7235+0.72798*P6
P7P	P7	32	0.841***	0.23737+0.76540*P7
P8P	P8	139	0.874***	-4.961+0.81905*P8
P9P	P9	32	0.894***	-4.003+0.79194*P9
P1	P2P	31	0.804***	13.157+0.88280*P2P
P2	P2P	32	0.845***	11.416+0.95943*P2P
P3	P4P	32	0.790***	14.584+0.90847*P4P
P4	P4P	32	0.809***	15.647+0.92755*P4P
P5	P5P	31	0.853***	19.730+0.88206*P5P
P6	P6P	31	0.856***	14.842+1.0066*P6P
P7	P8P	139	0.855***	25.818+0.85591*P8P
P8	P8P	139	0.874***	21.667+0.93208*P8P
P9	P9P	32	0.894***	17.210+1.0081*P9P

*p<0.05; **p<0.01; ***p<0.001

3.2 – Structural size and shape

A PCA was conducted with biometric measurements (lengths of wing, tail, bill and

tarsus) in order to assess general patterns of structural size and shape. The first three components explained successively 45.04%, 24.41% and 17.73% of variation in the data (Tab. 5). The first principal component (*bodyPC1*; Tab. 5) was highly negatively correlated ($p<0.001$) with all biometric variables; consequently, it was interpreted as an index of structural size. To facilitate interpretation of results, we multiplied individual scores of *bodyPC1* by -1, so that increasing values of *bodyPC1*(-) correspond to increasing values of structural size. Apart from correlations with the four morphological variables used to conduct this PCA, we also looked to its relation with body mass, an often used but unreliable measure of size, and found them to be significantly positively correlated ($r=0.519$, $p<0.001$). The second principal component, *bodyPC2* (Tab. 5), has low positive loadings with wing and tail length, and negative loadings with bill and tarsus length, being especially correlated with bill length ($r=-0.884$, $p<0.001$). Again, to facilitate interpretation of results, we multiplied individual scores of *bodyPC2* by -1, so that increasing values of *bodyPC2*(-) correspond to an increase in bill length (but also, in a small scale, of tarsus length) and a decrease in wing length and tail length. The third principal component, *bodyPC3* (Tab. 5), has a high positive correlation with tarsus length ($r=0.669$, $p<0.001$) and negative loading for the rest of the variables. These two factors are interpreted as components associated with structural shape variation.

Tab. 5 – Factor loadings for the three principal components of a PCA with lengths of wing, tail, bill and tarsus (n=339). Eigenvalues and percentage of total variance for each principal component are also shown.

	Factor loadings		
	bodyPC1	*bodyPC2*	*bodyPC3*
Wing length	-0.790***	0.290***	-0.064
Tail length	-0.748***	0.283***	-0.419***
Bill length	-0.361***	-0.884***	-0.287***
Tarsus length	-0.698***	-0.174**	0.669***
Eigenvalue	1.802	0.976	0.709
% of total variance	45.04%	24.41%	17.73%

*p<0.05; **p<0.01; ***p<0.001

3.3 – Wing shape

Primary feather lengths (Px) from all populations were used in a PCA to analyse components of wing size and shape variation. The first three components, *wingPC1*,

wingPC2 and *wingPC3* (Tab. 6), explained, respectively, approximately 86.55%, 7.47% and 2.58% of variation in the data. All primary feather length measures were highly negatively correlated ($p<0.001$) with *wingPC1* (Tab. 6), which leads us to interpret this as a component of wing size (decreasing values of *wingPC1* imply larger wings). As expected, *wingPC2* (Tab. 6) recovered a component of wing shape, namely roundness: proximal primary lengths (P1 to P5) have a positive loading on this component, while distal primary lengths (P6 to P9) have negative loadings. *wingPC3* has negative loadings associated with primaries P3 to P8, which we interpret as a component of wing concavity. In subsequent analysis we used individual scores of *wingPC2* as our index of wing shape. Since it's easier to interpret wing pointedness than wing roundness, we multiplied individual *wingPC2* scores by -1, making it an index of wing pointedness (higher scores of *wingPC2(-)* implying more pointed wings). The same was done in regards to *wingPC1*, in order to obtain a *wingPC1(-)* with increasing values related to increasing wing size. Despite being possible to interpret *wingPC3* in a biologically meaningful way, we will not consider it further because of its low eigenvalue.

Tab. 6 – Factor loadings for the first three principal components of a PCA with the length of each of the nine primary feathers (measured with a stopped-ruler), numbered descendantly (n=333). Eigenvalues and percentage of total variance for each principal component are also shown.

	Factor loadings		
	wingPC1	*wingPC2*	*wingPC3*
P1	-0.923***	0.303***	0.150**
P2	-0.940***	0.270***	0.126*
P3	-0.958***	0.223***	-0.011
P4	-0.963***	0.194***	-0.030
P5	-0.961***	0.084	-0.110*
P6	-0.956***	-0.048	-0.178**
P7	-0.925***	-0.316***	-0.135*
P8	-0.917***	-0.344***	-0.110*
P9	-0.822***	-0.439***	0.345***
Eigenvalue	7.789	0.672	0.233
% of total variance	86.55%	7.47%	2.58%

*p<0.05; **p<0.01; ***p<0.001

The index of wing size, *wingPC1(-)*, and the index of wing pointedness, *wingPC2(-)*, were compared (Pearson's correlation) to univariate biometric measurements and to the structural size and shape indices derived from the previous PCA, with the biometric variables, to assess relationships between them (Tab. 7). They were also compared to a set

of wing pointedness indices recovered from the literature, in order to assess the validity of these indices compared to the standard PCA multivariate approach, especially their relationship with *wingPC2(-)* (Tab. 7).

The index *wingPC1(-)* was highly significantly (p<0.001) correlated with lengths of wing, tail and tarsus, weight, *bodyPC1(-)*, *bodyPC2(-)* and the pointedness indices C2(-) and P1-P9. No significant relationship was found with the other variables. Regarding the comparison with biometric measurements and structural indices, *wingPC2(-)* was only significantly correlated with wing length (r=0.275, p<0.001), tail length (r=-0.122, p<0.05) and the structural shape index *bodyPC2(-)* (r=0.110, p<0.05). The size index *bodyPC1(-)* is not significantly (p>0.05) correlated with *wingPC2(-)*, the same happening with bill and tarsus length, as well as weight and the shape index *bodyPC3*. All the pointedness indices considered are highly significantly (p<0.001) correlated with *wingPC2(-)*, especially C2(-), P1-P9 and Kipp's index.

Tab. 7 – Correlation matrix of *wingPC1(-)* and *wingPC2(-)* against univariate biometric measurements, structural size and shape derived from a PCA and wing shape indices (n=326). Comparisons shown with respective coefficient of correlation (Pearson's r).

	wingPC1(-)	*wingPC2(-)*
Wing length	0.900***	0.275***
Tail length	0.530***	-0.122*
Bill length	0.096	-0.054
Tarsus length	0.401***	-0.081
Weight	0.379***	0.080
bodyPC1(-)	0.790***	0.028
bodyPC2(-)	-0.262***	-0.110*
bodyPC3	-0.054	-0.008
C2(-)	0.215***	0.896***
I5	-0.084	-0.611***
I9	0.080	0.360***
P1-P9	0.256***	0.861***
Kipp's (modified)	0.082	0.810***

*p<0.05; **p<0.01; ***p<0.001

3.4 – Migratory strategy classification

Of all 233 birds captured in the three continental sites, the application of the classification functions developed by de la Hera et al. (2007) to classify Iberian Blackcaps as migratory or sedentary was possible for 171 individuals (73.39%). The remaining 62 did not

have enough variables for the analysis to be performed. Birds from the Azores were not classified, as there's no evidence to suggest the occurrence of long-distance migration in those populations. Results indicate a high predominance of birds with migratory traits in all mainland sites sampled (Tab. 8). All age classes were well sampled for birds with migratory morphology, but the same cannot be said for birds with sedentary morphology, as only 2 adults (from PBG) were classified in this category. Regarding sex classes, 9 females and 21 males were recovered as sedentary, as well as 2 birds from RNLPT that had not yet undergone post-juvenile moult and thus could not be sexed. Birds classified as migrants comprise 60 females and 79 males. Since standardized sampling was not undertaken in ROM and PBG, no attempt will be made to analyse the variation of relative proportions of each class along time (migratory phenology).

Tab. 8 – Summary of results of the application of the migratory morphology classification functions (de la Hera et al., 2007) for the three continental sites sampled. Given in parenthesis are the numbers of individuals of the following three age classes: Adult/Juvenile-First-winter/Unknown. ROM – Paisagem Protegida Regional do Litoral de Vila do Conde e Reserva Ornitológica do Mindelo; PBG – Parque Biológico de Gaia; RNLPT – Reserva Natural Local do Paul de Tornada.

	Migratory	Sedentary	Unknown	**Total**
ROM	8 (2/3/3)	0 (-/-/-)	0 (-/-/-)	8
PBG	79 (31/41/7)	10 (2/6/2)	56 (16/38/2)	145
RNLPT	52 (10/39/3)	22 (-/21/1)	6 (2/4/-)	80
Total	139	32	62	233

3.5 – Morphological comparison of continental and island populations

Biometric data was collected at the 12 study sites with the aim of assessing trends in morphology associated with different geographic places of occurrence for the several populations. However, the considerable amount of possible categories for analysis would make it impractical to draw meaningful conclusions, so we considered five main groups for the analysis based on geographical occurrence and migratory behaviour. Kruskal-Wallis *H*-test using a set of morphological traits relevant for migration revealed the occurrence of significant differences in the groups for all of the morphological variables.

Looking at the results of each post-hoc multiple comparison test (Dunn's test) for the pairs of groups, we recover a complex pattern of morphological variation for univariate measures (Tab. 9 and Fig. 5). Wing length is significantly ($p<0.001$) smaller in continental sedentary birds when compared to all other groups, the opposite occurring in birds from

Corvo and Flores (Western Group), who have significantly ($p<0.001$) longer wings than other groups. Tail length is generally smaller in migrants, except when compared to sedentary birds; birds from the Western Group have tails that are significantly ($p<0.001$) longer than all other groups. Bill length has a complex pattern of variation, with significant differences when comparing shorter-billed birds from the Central Group with migrants ($p<0.05$), sedentary ($p<0.001$) and Western Group birds ($p<0.05$), as well as Eastern Group with sedentary birds ($p<0.001$), the latter with longer bills. Concerning tarsus length, Western Group birds presented again significantly longer tarsi than all other groups, with differing significance levels; apart from the differences to Western Group birds, continental sedentary individuals presented also significantly ($p<0.01$) shorter tarsi than the other Azores birds, but not significantly ($p>0.05$) shorter than migratory birds.

Tab. 9 – Comparison of Blackcap populations from five different geographical places of occurrence/migratory behaviour combinations for four different univariate (lengths of wing, tail, bill and tarsus) measures of morphology using a Kruskal-Wallis *H*-test. Dunn's post-hoc multiple comparison test was used to see pairs of groups with significant differences for each variable, (only z' values for pairs with significant differences are shown). M – Continental migrants; S – Continental sedentary; EG – Eastern Group (Azores); CG – Central Group (Azores); WG – Western Group (Azores).

	H	Dunn's test
Wing length (mm)	64.75***	S-M z'=6.36*** S-EG z'=7.65*** S-CG z'=5.10*** WG-M z'=3.53** WG-S z'=4.53*** WG-EG z'=4.24*** WG-CG z'=4.17***
Tail length (mm)	59.10***	M-EG z'=7.28* M-CG z'=3.40** M-WG z'=3.16*** WG-S z'=5.33*** WG-EG z'=4.28*** WG-CG z'=4.58***
Bill length (mm)	28.95***	S-EG z'=3.90*** CG-M z'=3.23* CG-S z'=4.46*** CG-WG z'=2.96*
Tarsus length (mm)	45.72***	S-EG z'=3.36** S-CG z'=3.41** WG-M z'=5.65*** WG-S z'=5.76*** WG-EG z'=3.22* WG-CG z'=3.51**

*p<0.05; **p<0.01; ***p<0.001

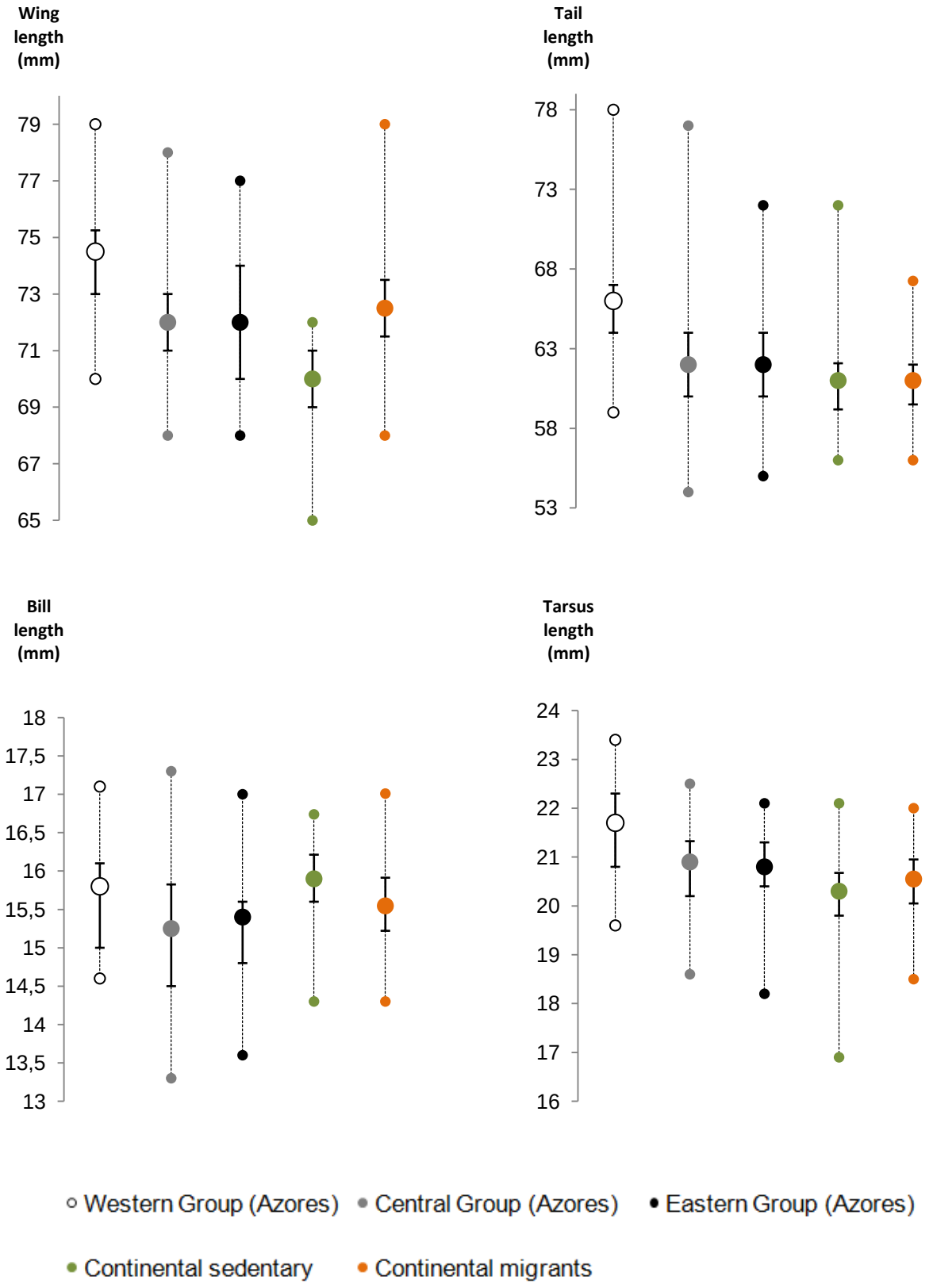

Fig. 5 – Comparison of Blackcap populations from five different geographical places of occurrence/migratory behaviour, for four different univariate (lengths of wing, tail, bill and tarsus) measures of morphology. Graphics show, for each population/variable, the median value of the observation, minimum and maximum values, while error bars denote the first and third quartiles.

In table 10 we present a summary of descriptive statistics of univariate measures for each geographical group of birds.

Tab. 10 – Summary of descriptive statistics of main univariate measures of morphology for Blackcaps from each geographical group under study. For each variable the following are shown: sample size (n), mean, standard error (SE), and maximum, median and minimum values.

		Continental migrants	Continental sedentary	Eastern Group (Azores)	Central Group (Azores)	Western Group (Azores)
Wing length (mm)	n	139	32	57	81	28
	Mean	72.69	69.83	72.19	72.28	74.36
	SE	0.172	0.304	0.299	0.225	0.368
	Max.	79.0	72.0	77.0	78.0	79.0
	Median	72.5	70.0	72.0	72.0	74.5
	Min.	68.0	65.0	68.0	68.0	70.0
Tail length (mm)	n	139	32	61	84	33
	Mean	60.74	61.04	62.36	62.27	66.03
	SE	0.166	0.515	0.442	0.377	0.738
	Max.	67.3	72.0	72.0	77.0	78.0
	Median	61.0	61.0	62.0	62.0	66.0
	Min.	56.0	56.0	55.0	54.0	59.0
Bill length (mm)	n	139	32	61	84	33
	Mean	15.57	15.84	15.31	15.19	15.69
	SE	0.044	0.101	0.096	0.094	0.121
	Max.	17.0	16.7	17.0	17.3	17.1
	Median	15.5	15.9	15.4	15.3	15.8
	Min.	14.3	14.3	13.6	13.3	14.6
Tarsus length (mm)	n	139	32	61	84	33
	Mean	20.51	20.14	20.77	20.78	21.55
	SE	0.056	0.177	0.103	0.089	0.165
	Max.	22.0	22.1	22.1	22.5	23.4
	Median	20.6	20.3	20.8	20.9	21.7
	Min.	18.5	16.9	18.2	18.6	19.6

The distribution of birds from the five study groups along the two first principal components resulting from the application of PCA on body measurements (lengths of wing, tail, bill and tarsus) is presented in figure 6. Differentiation in body morphology is mostly evident in the structural size axis (*bodyPC1(-)*), with birds from the Western Group with higher values in this component, and most continental sedentary birds grouped together at low values of this variable. Along the first shape component (*bodyPC2(-)*), most populations seem relatively similar.

Analysing each of these body structural indices (Tab. 11 and Fig. 7), in *bodyPC1(-)* significant differences were found in regards to the small structural size of continental sedentary birds when compared to birds from the Azores (sedentary continental birds tend also to be smaller when compared to migrants, but not significantly), and the significantly

(p<0.001) bigger structural size values of birds from the Western Group when compared to all the other four groups. *bodyPC2(-)* values were significantly higher in sedentary birds than in all other populations, and also different in the pair of groups continental migratory-Central Group, for which migrants had significantly (p<0.05) higher values of *bodyPC2(-)*. For *bodyPC3* only one significant (p<0.05) difference was found, between birds from the Central Group and sedentary birds from the continent, the latter with smaller values of this structural shape index.

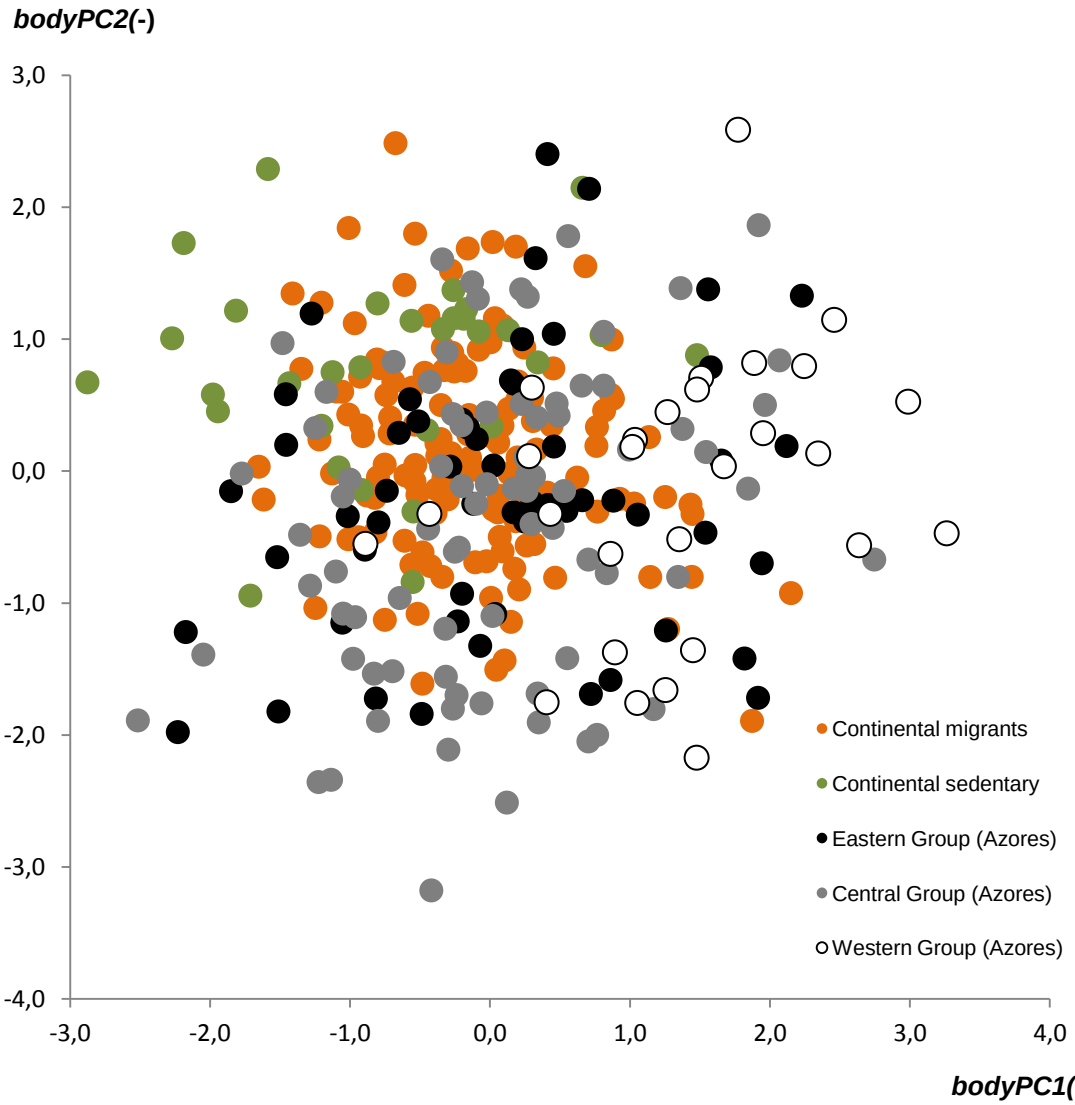

Fig. 6 – Plot of scores for the two principal components derived from a PCA with lengths of wing, tail, bill and tarsus as variables: *bodyPC1(-)*, a structural size index, and *bodyPC2(-)*, an index of structural shape mostly associated with increases in bill size, for continental migrants, continental sedentary and birds from the Azores (Eastern, Central and Western groups).

Tab. 11 – Comparison Blackcap populations from five different geographical places of occurrence/migratory behaviour combinations for three different multivariate measures of body morphology (*bodyPC1(-)*, *bodyPC2(-)* and *bodyPC3*) using a Kruskal-Wallis *H*-test. Dunn's post-hoc multiple comparison test was used to see pairs of groups with significant differences for each variable, (only z' values for pairs with significant differences are shown). M – Continental migrants; S – Continental sedentary; EG – Eastern Group (Azores); CG – Central Group (Azores); WG – Western Group (Azores).

	H	Dunn's test		*H*	Dunn's test
bodyPC1(-)	56.59***	S-EG z'=3.55** S-CG z'=3.32** WG-M z'=6.35*** WG-S z'=7.14*** WG-EG z'=4.61*** WG-CG z'=5.27***	***bodyPC2(-)***	36.88***	M-CG z'=3.13* S-M z'=3.69** S-EG z'=4.88*** S-CG z'=5.56** S-WG z'=3.90***
			bodyPC3	11.15*	S-CG z'=3.14*

*p<0.05; **p<0.01; ***p<0.001

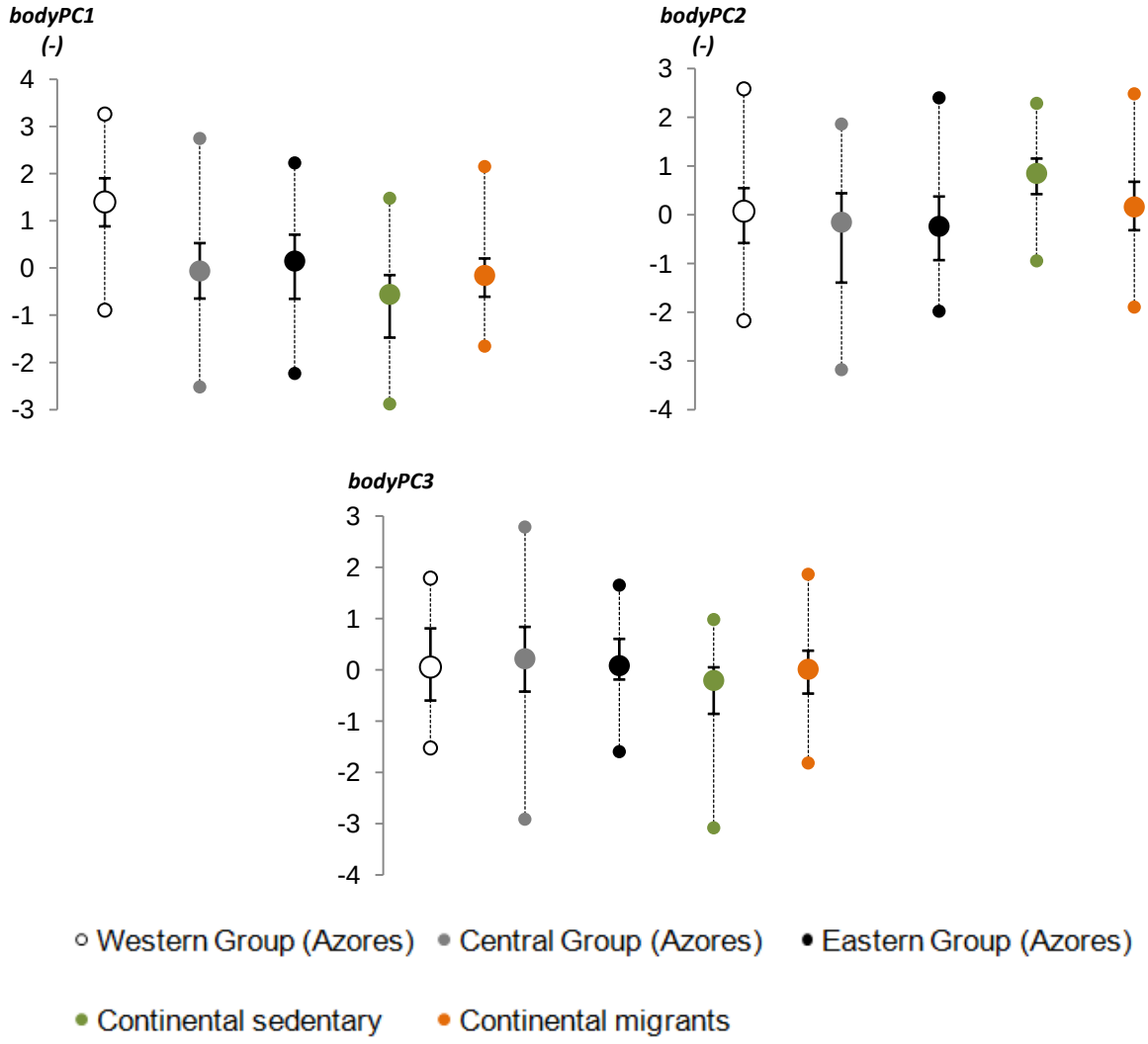

Fig. 7 – Comparison of Blackcap populations from five different geographical places of occurrence/migratory behaviour, for three different multivariate measures of body morphology (*bodyPC1(-)*, *bodyPC2(-)* and *bodyPC3*). Graphics show, for each population/variable, the median value of the observation, minimum and maximum values, while error bars denote the first and third quartiles.

The distribution of birds from the five study groups along the two first principal components resulting from the application of PCA on wing primary lengths is presented in figure 8. Continental sedentary birds tend to present low values of both *wingPC1(-)* and *wingPC2(-)*, which suggests smaller and less pointed wings than the other groups. Continental migrants show a tendency for large and pointed wings. Although island birds seem to share some overall characters, Western Group birds (from the islands of Corvo and Flores) stand out with particularly large and less pointed wings.

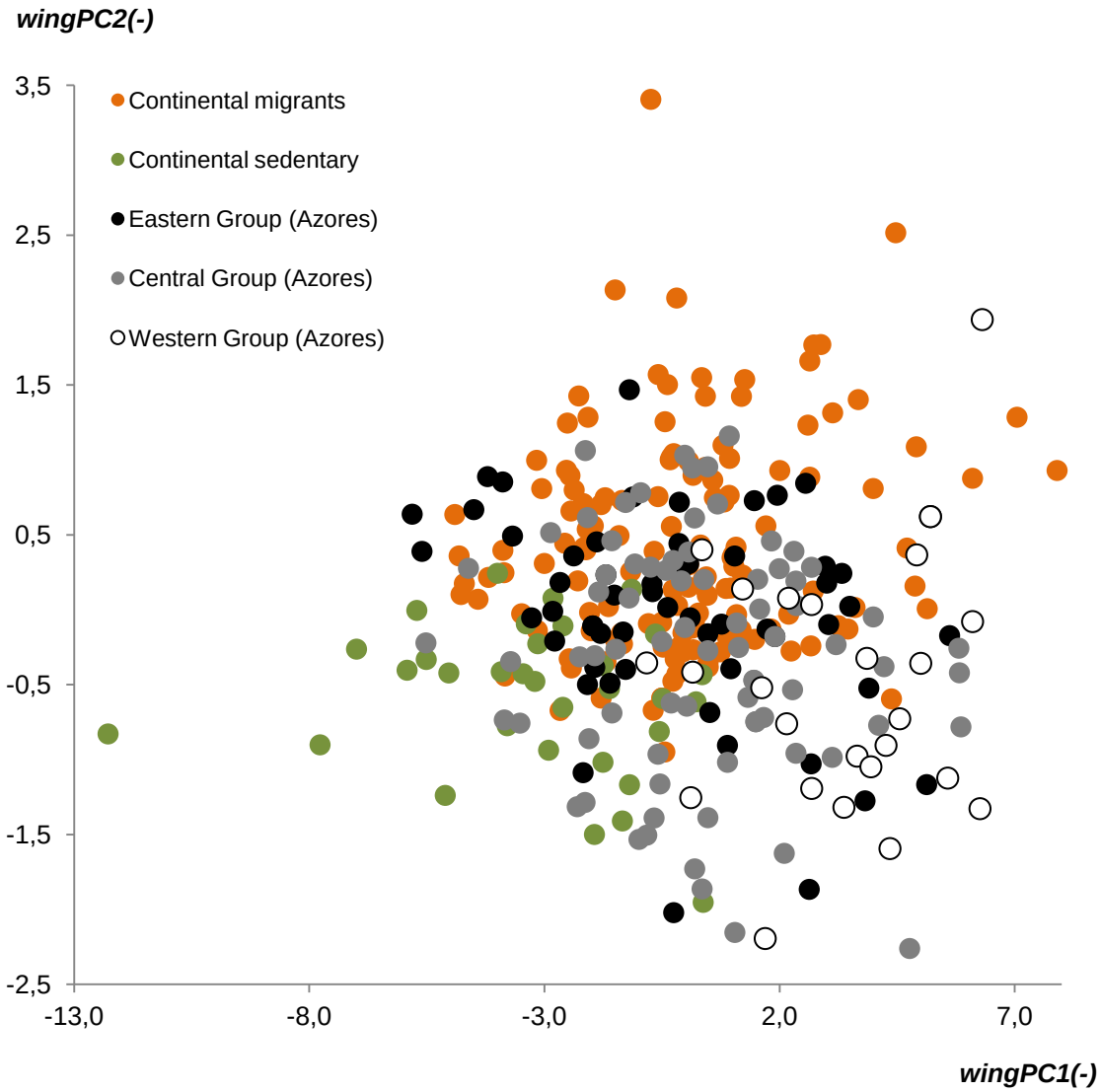

Fig. 8 – Plot of scores for the two principal components derived from a PCA of primary feather lengths (multiplied by -1 for ease of interpretation): *wingPC1(-)*, an index of increasing wing size, and *wingPC2(-)*, an index of increasing wing pointedness, for continental migrants, continental sedentary and birds from the Azores (Eastern, Central and Western groups).

Therefore, analysis of these multivariate indices results reveals patterns of variation (Tab. 12 and Fig. 9) similar to those previously described for univariate measures. The values of the index of wing size *wingPC1(-)* revealed significant ($p<0.001$) differences in two groups in comparison to all others: continental sedentary birds had significantly smaller wings, the opposite occurring in birds from Corvo and Flores, who tend to have bigger wings than all other populations. Regarding wing pointedness, continental migrants had values of *wingPC2(-)* that were significantly different from all other groups considered, the higher values indicating more pointed wings for this group; the analysis didn't find any significant differences ($p>0.05$) for the other pairs of groups for this variable, except for the pair continental sedentary birds-Eastern Group birds, which were significantly different ($p<0.01$). The group that includes birds from Santa Maria and São Miguel was furthermore the non-migrating group with higher values of *wingPC2(-)*, with a lower significance value when compared to continental migrants ($p<0.05$ versus $p<0.001$ in comparison with other Azores birds).

Tab. 12 – Comparison of Blackcap populations from five different geographical places of occurrence/migratory behaviour combinations for two different multivariate measures of wing morphology (*wingPC1(-)*, *wingPC2(-)* using a Kruskal-Wallis *H*-test. Dunn's post-hoc multiple comparison test was used to see pairs of groups with significant differences for each variable, (only z' values for pairs with significant differences are shown). M – Continental migrants; S – Continental sedentary; EG – Eastern Group (Azores); CG – Central Group (Azores); WG – Western Group (Azores).

	H	Dunn's test
wingPC1(-)	70.99***	S-M z'=5.21*** S-EG z'=4.41*** S-CG z'=5.66*** S-WG z'=8.30*** WG-M z'=5.46*** WG-EG z'=5.14*** WG-CG z'=4.45***
wingPC2(-)	77.00***	M-S z'=6.88*** M-EG z'=3.18* M-CG z'=6.07*** M-WG z'=5.17*** S-EG z'=3.85**

*p<0.05; **p<0.01; ***p<0.001

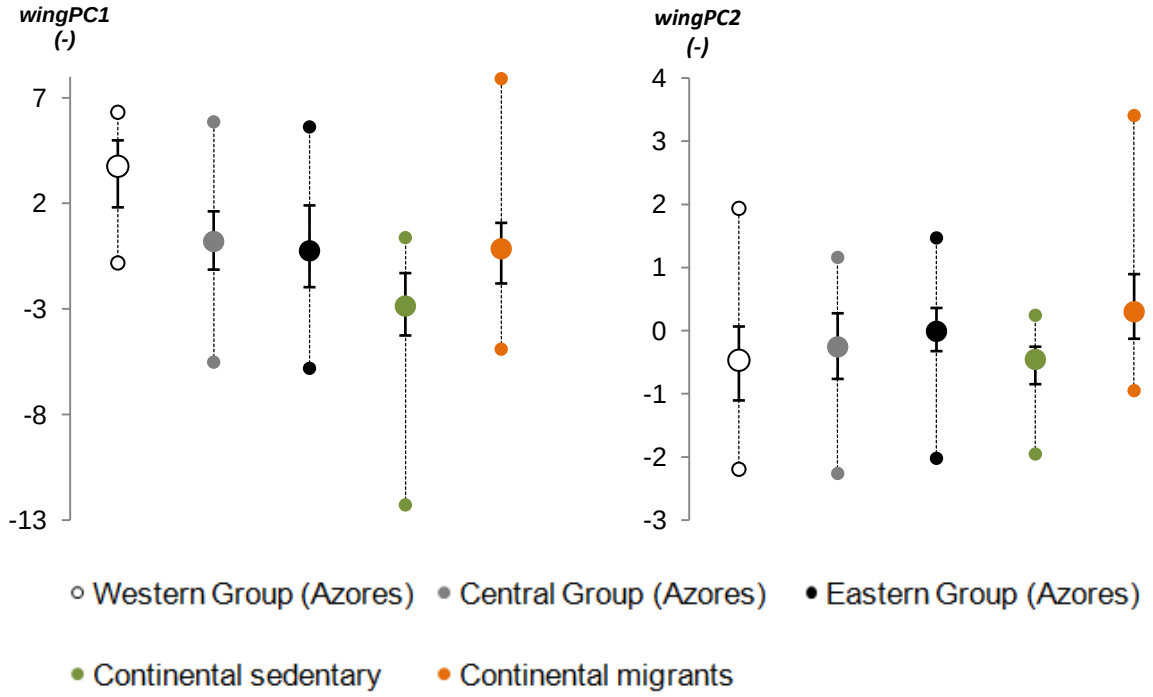

Fig. 9 – Comparison of Blackcap populations from five different geographical places of occurrence/migratory behaviour, for two different multivariate measures of wing morphology (*wingPC1(-)* and *wingPC2(-)*). Graphics show, for each population/variable, the median value of the observation, minimum and maximum values, while error bars denote the first and third quartiles.

Regarding the effect of island physical characteristics (Tab. 13 and Figs. 10 to 13), the area (km^2) was significantly ($p<0.05$, or higher) correlated with wing length, tarsus length, weight, *bodyPC1(-)* and *wingPC1(-)*. Increasing distances to the continent (km) were significantly correlated ($p<0.05$, or higher) with all the univariate measures, *bodyPC1(-)*, *wingPC1(-)* and *wingPC2(-)*. The correlation between distance to the mainland and the pointedness index *wingPC2(-)* was the only significant inverse relation ($r=-0.220$, $p<0.01$) between variables in this comparison.

Tab. 13 - Correlation matrix of island physical geography descriptors (area and distance to mainland) against univariate biometric measurements, structural size and shape derived from a PCA and wing shape indices, from Blackcap populations of the nine Azores islands. Comparisons shown with respective coefficient of correlation (Pearson's r), with valid n in parenthesis.

	Wing length (mm)	Tail length (mm)	Bill length (mm)	Tarsus length (mm)	Weight (g)	*bodyPC1 (-)*	*bodyPC2 (-)*	*bodyPC3*	*wingPC1 (-)*	*wingPC2 (-)*
Area (km^2)	0.227** (n=166)	0.119 (n=178)	0.204** (n=178)	0.131 (n=178)	0.211** (n=178)	0.254*** (n=166)	0.128 (n=166)	0.074 (n=166)	0.168* (n=162)	0.036 (n=162)
Distance to mainland (km)	0.300*** (n=166)	0.293*** (n=178)	0.154* (n=178)	0.302*** (n=178)	0.386*** (n=178)	0.348*** (n=166)	0.015 (n=166)	0.022 (n=166)	0.413*** (n=162)	-0.220** (n=162)

*p<0.05; **p<0.01; ***p<0.001

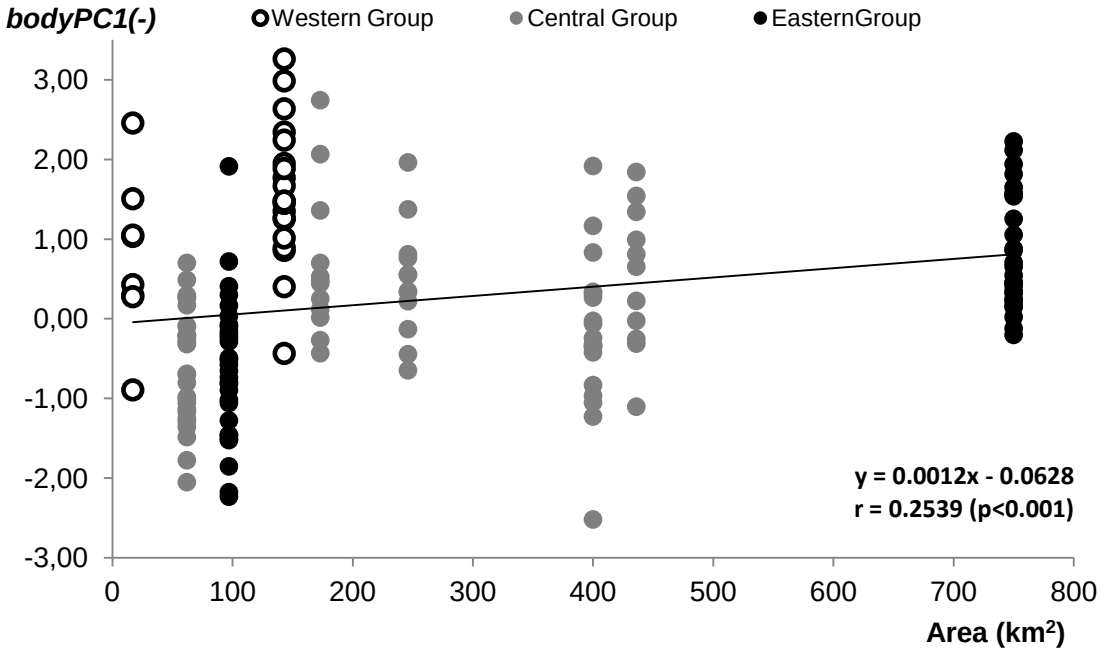

Fig. 10 – Correlation plot between the index of structural size *bodyPC1(-)* and island area (km^2) for the Blackcap populations sampled from the nine islands of the Azores, indicating a low, but highly significant, correlation (r=0.254, p<0.001) between island area and insular birds' body size.

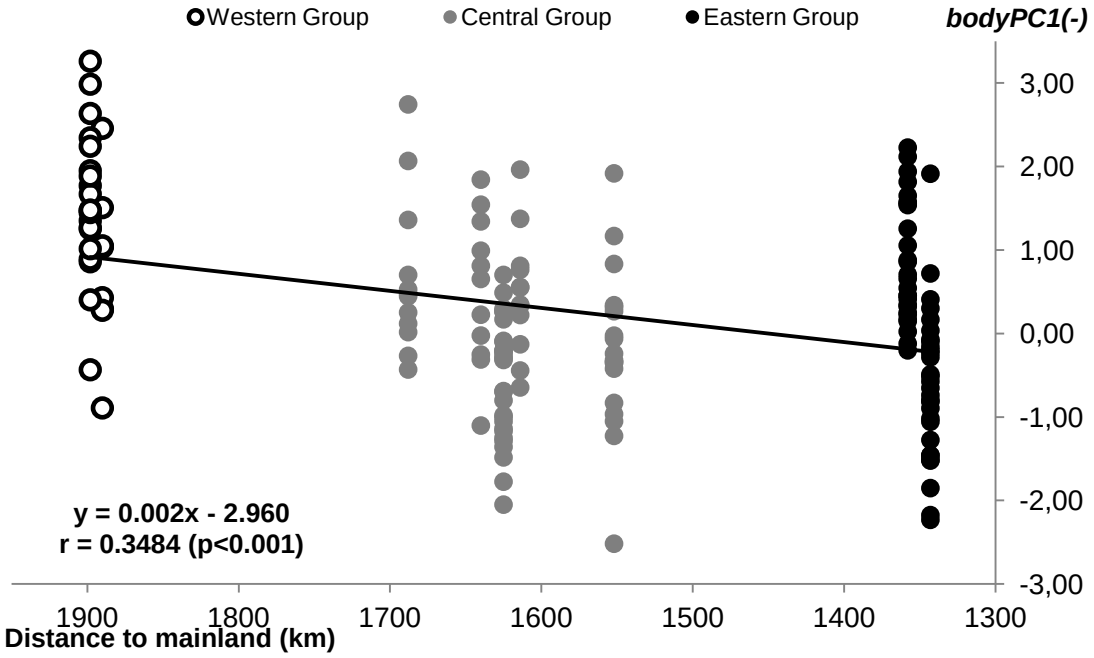

Fig. 11 – Correlation plot between the index of structural size *bodyPC1(-)* and the distance to continental Portugal (km) for the Blackcap populations sampled from the nine islands of the Azores, indicating a low, but highly significant, correlation (r=0.348, p<0.001) between island isolation and insular birds body size. The distance axis is inverted (values increase from right to left) to indicate the location of the islands along an East-West longitude axis.

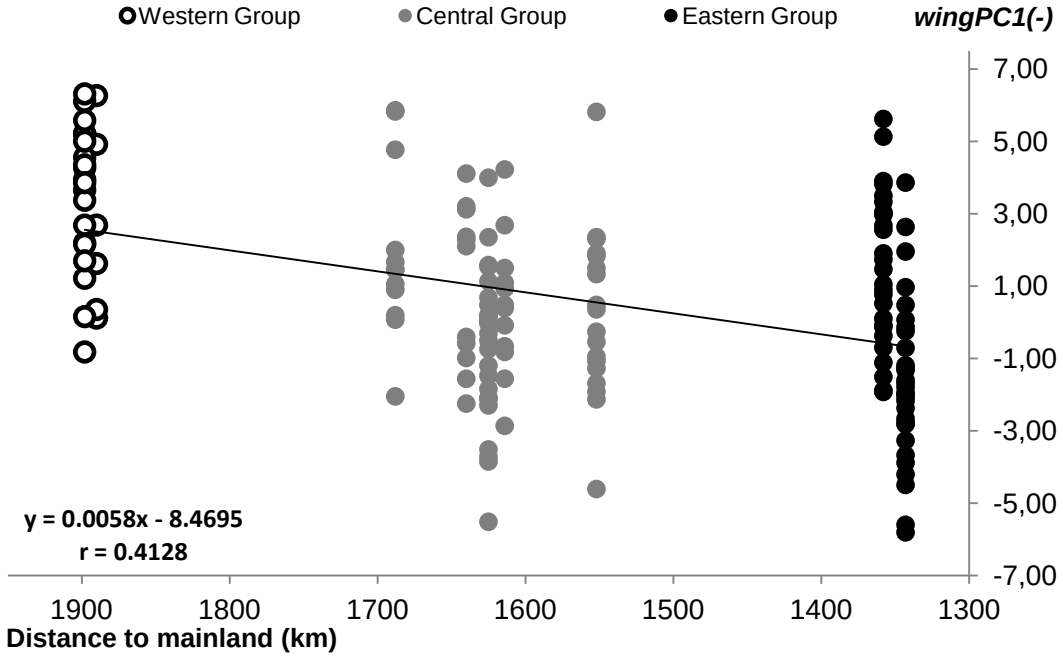

Fig. 12 – Correlation plot between the index of wing size *wingPC1(-)* and the distance to continental Portugal (km) for the Blackcap populations sampled from the nine islands of the Azores, indicating a low, but highly significant, correlation (r=0.413, p<0.001) between isolation and wing size of insular Blackcap populations. The distance axis is inverted (values increase from right to left) to indicate the location of the islands along an East-West longitude axis.

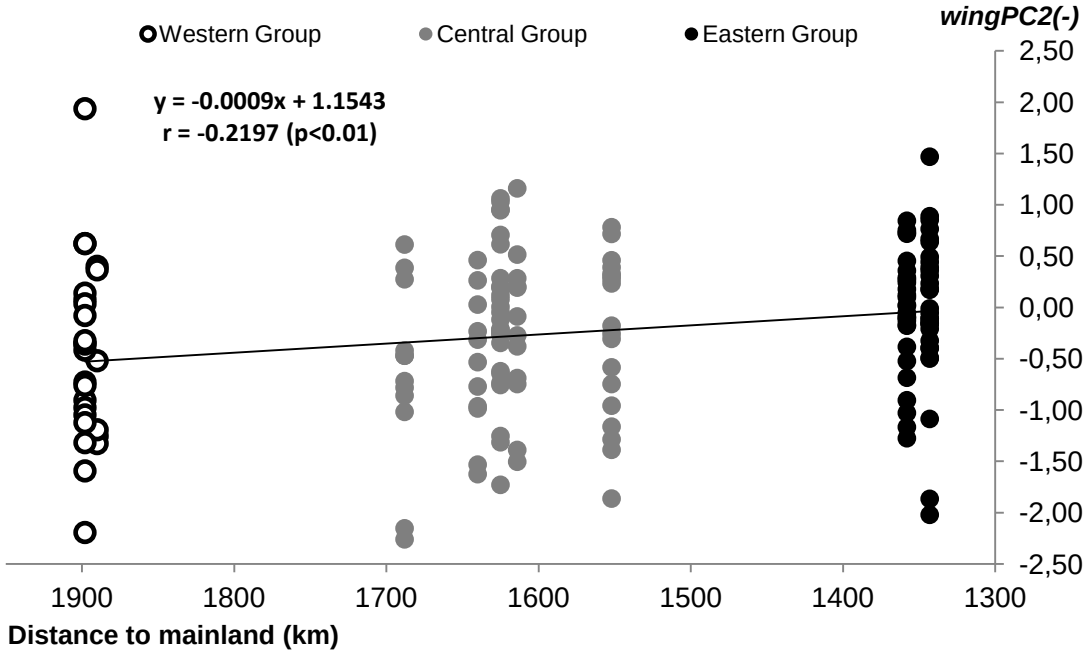

Fig. 13 – Correlation plot between the index of wing pointedness *wingPC2(-)* and the distance to continental Portugal (km) for the Blackcap populations sampled from the nine islands of the Azores, indicating a low, but significant, inverse correlation (r=-0.220, p<0.01) between isolation and wing shape of insular Blackcap populations. The distance axis is inverted (values increase from right to left) to indicate the location of the islands along an East-West longitude axis.

4 – Discussion

4.1 – Univariate morphological measures

Our results on the analysis of biometric measurements in the five study populations show similar trends as those found in previous studies. Continental migrants have longer wings than continental residents, as was expected, since this is an often recovered result in these comparisons (although some contradicting results have been found, see Mulvihill & Chandler, 1991, Pérez-Tris & Tellería, 2001, Voelker, 2001, Egbert & Belthoff, 2003). Longer wings are usually related with a higher aspect ratio of the wing, which improves aerodynamic efficiency. Continental sedentary birds actually have shorter wings than all other groups, including sedentary island groups from the Azores, what is in accordance with some other studies that have also found that island populations have longer wings (Clegg et al., 2008, Wright & Steadman, 2012). This is especially pronounced in birds from the Western Group, which have particularly long wings, even when compared to migrants. In other studies that also compare different Blackcap populations (Fitzpatrick, 1998, Fiedler, 2005), similar trends were recovered, with Northern European migrants having longer wings, and one group of island birds with very long wings, namely Cape Verde birds, which according to morphological characters are usually classified in the same subspecies as Azores Blackcaps, *S. a. gularis*. The longer wings of Western Group birds are probably explained by an increase in body size, instead of reflecting modifications to the wing morphology.

Although the differences are not significant, migrants show a tendency to have shorter tails than all other populations, which is a similar result to the obtained by Tellería & Carbonell (1999). If shorter tails aid in reducing drag in forward flight, and long tails aid in manoeuvrability, these patterns are to be expected. Also, Azorean birds have longer tails, which could both be related to increases in overall size but also adaptations to habitat use. One of the most common trends in the evolution of island bird populations is the increase in bill length, but our results show a different picture, with island groups usually with shorter bills, except for birds from the Western Group, but again this probably indicates an effect of overall size. From the continental birds, although the differences are not significant, residents tend to present longer bills than migrants. Differences in tarsus length are also not significant between continental residents and migrants. The generally longer tarsi of island birds (especially when compared to continental residents) are in agreement with many other studies in adaptation to island habitats (Grant, 1979, Carrascal et al., 1994, Komdeur et al.,

2004, Wright & Steadman, 2012).

Presenting the patterns of univariate measurements is helpful when comparing with many other studies in which single measurements have been used to assess patterns of morphological change associated with island colonisation by birds or the effect on morphology of different migratory behaviour. However, we feel that its usefulness is rather limited because analysing single measurements does not eliminate the effects of size, and thus it is not possible to ascertain if a body part changes size as a function of different size or shape in the various populations under study. When analysing the patterns of morphological change in each variable independently in our five Blackcap populations, this problem appeared several times. Therefore, we feel the analysis of morphology aided by multivariate methods give a truer picture of the morphological differences encountered among different Blackcap populations in continental and island settings.

4.2 – Structural size and shape

The application of a principal component analysis using the lengths of wing, tail, bill and tarsus as variables recovered one main component which we interpret as a component of size (Rising & Somers, 1989). After multiplying by -1 to facilitate interpretation of results, increasing values of *bodyPC1(-)* correspond to an increase in structural size. This result is analogous to most other results of principal components analysis aimed at getting indices of structural size in birds (Senar & Pascual, 1997, Tellería & Carbonell, 1999, Calmaestra & Moreno, 2001, Pérez-Tris & Tellería, 2001, Pérez-Tris et al., 2003, Scott et al., 2003, Kaboli et al., 2007, Clegg et al., 2008, Milá et al., 2008, Mathys & Lockwood, 2009, Baldwin et al., 2010, Wright & Steadman, 2012), which recover the first component as an index of size. In the five study populations, birds from the Azores tend to show higher *bodyPC1(-)* scores than continental birds, especially for birds from the Western Group. These have significantly higher values of *bodyPC1(-)* than all other study groups, and results indicate a positive highly significant correlation between distance to mainland and increasing structural sizes, albeit with a relatively low correlation value. According to the island rule, there is a trend towards larger body sizes in island populations in small vertebrate taxa, so these results point to the confirmation of this trend in regards to the structural body size of Blackcaps for the Azores. The islands of the Western Group are the ones furthest apart from continental Portugal (the average distance from these two islands to continental Portugal is approximately 1861 km), as well as having the lowest combined area of the three groups (approximately 160 km^2).. Increases in structural size were poorly related to increases in island area. In smaller islands

available resources are usually scarcer, which would select for animals with smaller size in order to decrease energy expenditure (McNab, 2002, Boyer & Jetz, 2010). Possibly the size of insular Blackcap populations can be explained by both ecological release and resource limitation. Vertebrate communities in the Azores are much poorer when compared to the mainland (Borges et al., 2010, Catry et al., 2010), which would mean decreased interspecific competition when compared to continental habitats, and thus larger overall sizes. Within the insular setting, however, high intraspecific competition may select for smaller body sizes with decreases in island area (and thus, of available resources). When correlations between island area and structural size are done individually for each island group (thus eliminating much of the effect of distance to the mainland on size), the pattern of increasing size with increasing island area still stands, which further supports this assertion. However our data suggest a stronger effect of distance rather than island area on the size of Azorean Blackcaps.

Also highlighting these trends is the highly significant difference in size between continental sedentary populations and sedentary birds from all island groups. The latter have higher values of the structural size index *bodyPC1(-)*. This is especially relevant since all are non-migratory populations from similar latitudes, so make a good case to compare morphological differences related to the colonisation of island habitats. Although island colonization was probably done by migrants, previous results indicate northwest Iberian Blackcaps are closely related to both western European migrants and Atlantic island populations (see Pérez-Tris et al., 2004, Dietzen et al., 2008 and Rodrigues, 2012). In this particular case, our results support the trend towards larger body size in small bird island populations.

Apart from the differences with birds from the Western Group, migrants do not show significant size differences compared to island populations or continental sedentary birds. Migratory Blackcaps passing through, or wintering in Iberia can originate from Western European breeding grounds of varying latitudes (Cantos, 1995). Also, as Blackcaps with different distances of migration possess different characteristics (Fiedler, 2005), our migratory sample probably includes birds from different parts of the existing geographical ecomorphological gradient (according to Bergmann's rule). Meiri & Dayan (2003) have noted that Bergmann's rule is a general trend that applies to most bird groups, but especially in sedentary species, given that they do not vacate higher latitudes during the winter (in migratory species Bergmann's rule still applies, but with less frequency). Tellería & Carbonell (1999) found Iberian Blackcap residents to be larger than migrants, contradicting our results, but their migratory population consisted entirely of birds with a North Iberian origin. Thus, the

effect of larger size with increasing latitudes (Bergman's rule) is probably not represented in their sample, and is thus a better picture of the size relationships of birds with different migratory behaviour but only from Iberia. Hence, the presence of larger migrants from Northern Europe could be influencing the result of no size differences between continental migrants and the other study groups (continental sedentary birds tend to be smaller but not at a significant level). Additionally, as Pérez-Tris et al. (1999) and de la Hera et al. (2007) have noted, the main shortcoming in their classification functions is the classification of a smaller portion of sedentary birds as migratory, so this could also be giving a misleading picture of the differences between migrants and continental residents. Apart from the distinction between continental migrants and residents provided by the discriminating function proposed by these authors, and not considering genetic or isotopes analysis, there is currently (to our knowledge) no way to distinguish migratory populations of Blackcap from different geographical origin in order to overcome this limitation, unless they were to be measured at their different breeding sites.

The other two components, *bodyPC2(-)* and *bodyPC3*, have opposing loadings on different variables, so we interpret them as components of shape. The index *bodyPC2(-)* is positively correlated with bill (mostly) and tarsus lengths, and negatively with wing and tail lengths. A direct interpretation of this shape index is not straightforward, and could be related to a number of ecological constraints suffered by different Blackcap populations. Analysing the pattern of this index among our study groups, we find that continental sedentary birds stand out, with significant differences when compared to all other groups (significantly higher values of *bodyPC2(-)*). The only other significant difference is found when comparing continental migrants to birds from the Central Group, these with lower values. Although not always significantly so, birds from the Azores have lower values of *bodyPC2(-)* than the two continental groups. Thus, *bodyPC2(-)* could be an index of structural shape change associated with sedentarization in Iberian Blackcaps. Apart from the observation that this index has mostly significant differences in continental sedentary birds to all other groups, the opposing signs between flight apparatus variables (wing and tail lengths) and traits associated with habitat use (bill and tarsus lengths) suggests this as well. Under this size-independent component, continental sedentary birds have longer tarsi, which may be useful for moving within dense vegetation in search of food or evading predators, while the reduced size of the tarsi in migratory individuals may be useful in reducing parasitic drag in long-distance flight (Hedenström, 2002). In an interspecific study of the relationships between foraging habits and morphology in some Iberian insectivores (not including the Blackcap), Carrascal et al. (1990) found that longer bill and tarsi are associated with foraging among

foliage and in bushes. Sedentary and migrant Blackcaps in Iberia vary slightly in their wintering habitat preferences (Pérez-Tris & Tellería, 2002), with the former almost restricted to forests, while their migratory conspecifics can also be found in high numbers in shrubland, given that they don't need to protect the best breeding territories. Food choice was also slightly different (Tellería et al., 2013), as migrants have a more varied winter diet, with a higher percentage of invertebrates than residents, who consume mostly fruits. However, these authors have also found that the bigger bill size in sedentary birds does not mean they consume bigger fruit, so the relationships between bill morphology and foraging behaviour in the Blackcap have yet to be fully understood. It is also interesting that, if *bodyPC2(-)* is indeed related to sedentarization in Iberian Blackcaps, Azores birds have lower values of this index, which indicates that sedentarization in this island system results in different ecomorphological adaptations related to habitat use and resource foraging.

The shape component *bodyPC3* is also difficult to interpret, especially since the only significant difference was found between continental sedentary birds and individuals from the Central Group. This component is associated with increasing tarsus length, and values are higher in birds from the Azores. An increase in the length of hind limb elements is usually associated with more terrestrial modes of habitat use in birds (Zeffer et al., 2003), and with the niche expansion expected in island birds, this can result in increased ground foraging. This tendency for ground foraging has been noted for Macaronesian Blackcaps. Bourne (1955) noticed a number of slight differences in behaviour of Cape Verde Blackcaps and European populations, notably a marked tendency for the former to forage on the ground, which is unusual in their continental conspecifics. Buxton (1960) recorded similar behaviour in birds from Madeira. As discussed previously, ecological release from interspecific competition can be a driver of morphological change in insular vertebrate taxa, as reduced community diversity enables insular species to adapt to more generalistic foraging modes. The higher values of *bodyPC3* in Blackcaps from the Azores could indicate this broadening of foraging strategies. Previous work (Neves et al., 2004) on the ecology of Blackcaps from the island of Pico indicates a generalistic feeding approach in birds from this island. Carrascal et al. (1990), however, point that increases in tarsometatarsus length do not correlate with ground foraging habits in insectivorous species that inhabit similar habitats to Blackcaps in Iberia. Combined with the general absence of significant differences in this component between insular and continental Blackcaps, it is not possible for now to safely assume differences in foraging behaviour in birds from the Azores result in morphological changes.

4.3 – Wing shape

The first component recovered from a PCA on primary feather lengths, after multiplying by -1, gave us an index of increasing wing size, *wingPC1(-)*. The pattern of correlation with other variables suggest that wing size is related to overall body size, as this index is highly significantly correlated with increases in most univariate measures, and also increases in the structural body size index *bodyPC1(-)*. Interestingly, it was also correlated (inversely) with the structural shape component *bodyPC2(-)*, which we identified previously as a component possibly related with morphological adaptations to sedentarization in Iberian Blackcaps. Differences in *wingPC1(-)* were found mostly in continental sedentary birds, which thus present significantly smaller wings than all other groups, and between Western group birds, which had significantly larger wings than all other groups. There is a trend from nearest to farthest island system from the continent of increasing wing size. This difference is only significant in the comparison of Western Group with the others, but a significant correlation is recovered. These results were similar to the results encountered with *bodyPC1(-)*, which further supports that wing size in Blackcap varies mostly according to overall size changes. The only relevant difference is that continental residents are not significantly smaller (structural size) than migrants, but their wings are significantly smaller. As wing size is highly correlated with wing length, significantly higher values of *wingPC1(-)* in migrants are probably related to modifications in wing length to increase aerodynamic performance.

As in some other similar studies (Chandler & Mulvihill, 1988, Chandler & Mulvihill, 1990, Lockwood et al., 1998, Egbert & Belthoff, 2003, Peiró, 2003, Pérez-Tris et al., 2003, Alonso & Arizaga, 2006), after the first component removes size-related variation, the second component is related to increases in wing pointedness. *wingPC2(-)* was highly significantly correlated with all the wing pointedness indices tested, which assures the validity of comparisons of our work with previous studies on this topic (even when no multivariate approaches were taken in these). Most of these indices have been used frequently in the literature, and although they can successfully represent wing shape, their use has been replaced by more reliable multivariate techniques (Chandler & Mulvihill, 1988, Lockwood et al., 1998). Our results thus show that, under the impossibility of performing multivariate analysis techniques to analyse wing shape, simple indices may still provide adequate results. Specifically, we would like to note the high value of correlation between *wingPC2(-)* and the P1-P9 index proposed by Pérez-Tris et al. (1999). This index has not been widely used in the literature, but we find that, at least in the Blackcap populations we sampled, it is very

effective in representing wing pointedness.

Wing pointedness, as represented by *wingPC2(-)*, was also highly significantly correlated with wing length, indicating that birds with pointed wings tend to have longer wings, as is usually the case with migrants. However, the relatively low correlation value points that caution should be taken whenever wing length alone is used as an indication of migratory status of an individual bird. The significant inverse correlations of *wingPC2(-)* with tail length and *bodyPC2(-)* are also expected since long distance migrants usually have both pointed wing and shorter tails, while migrants in our sample also have lower values of *bodyPC2(-)* than continental sedentary birds. When we analyse the scores of this index for the five study groups, migrants have significantly different values than all other populations, which again points to the importance of a pointed wing to improve forward flight performance during migration. For the other groups, the lowest values were found for continental sedentary birds (which thus have the roundest wings), but these were only significantly smaller than those of migrants and birds of the Eastern Group. It is known for island Blackcaps to have relatively pointed wings, as birds from the Madeira island are known to have intermediate pointedness scores between Central European and Mediterranean populations (Fiedler, 2005). Overall, the lack of significant differences between wing pointedness in continental sedentary birds and most birds from the Azores could reflect morphological adaptation to non-migratory behaviour, irrespective of the setting.

Even if no significant differences were found between the values of *wingPC2(-)* for the three island groups, there seems to be a graded trend towards less pointed wings from the Eastern to the Western groups. While increasing wing size in the more distant islands make sense under the ecological release hypothesis, as wing size is related to structural size, it is not immediately clear why birds from distant islands should have rounder wings given that, according to molecular studies, all Azores populations are putatively sedentary and there is no significant gene flow occurring between continental and Azorean birds. However, if we consider the possibility of regular movements occurring between continental and island populations, this is a wing shape pattern that we could expect to arise. In more distant islands the probability of successfully travelling from and to the continent is reduced, so selection towards rounder wings could occur. If the nearest islands receive individuals from the continent on a more regular basis, we should expect to sample birds with more pointed wings.

5 – Conclusions

Understanding the way in which different selective pressures created by migration, sedentarization and insularity shape bird morphology has been a key topic in avian ecomorphological studies. Although patterns of morphological change associated with migration in the Blackcap are well known, few studies (Fiedler, 2005, Dietzen et al., 2008, Rodrigues, 2012) have centered on the morphological adaptations to insularity in this bird, one of the best studied passerine model species.

Our results show yet more support for many predictions for migratory morphology, namely that, when compared to residents, migrants have relatively longer, more pointed wings, shorter bills and shorter tails. Although our migratory sample tend to have larger tarsi , this is probably a reflection of larger structural sizes, as sedentary birds had significantly higher values in the first shape component correlated with tarsus length. The larger structural body size of the migrants is probably a reflection of Bergmann's rule, which states that animals from higher latitudes tend to be larger, especially since our migratory sample does not discriminate the origin of birds. In a previous study (Tellería & Carbonell, 1999) in which the origin of the migrants was known, and close to the sedentary population range, migrants had on average smaller structural sizes, which are probably better suited to decrease energy expenditure in long migratory flight.

Despite much discussion centered on the validity of the predictions of the island rule, the patterns of change in Azores Blackcaps give some support to this model, especially when compared to continental residents from northwest Portugal. This is probably the best comparison group given that they all include non-migratory populations and that colonization possibly occurred from this geographic region (Pérez-Tris et al., 2004, Dietzen et al., 2008, Rodrigues, 2012). Continental sedentary birds were significantly smaller than Azores populations, both in terms of structural size, wing size, wing length and tarsus length. This suggests the accuracy of predictions that state that in the face of reduced interspecific competition compared to the mainland, small insular vertebrates increase in size. Also highlighting this are the trends of increased size with increases in distance to the mainland. The observed trend of increase in structural size with increases in area is weak. The decreases in island area can result in higher (beneficial in intraspecific disputes) or smaller (which require less energy) sizes. Subtle, non-significant differences are also found in regards to wing shape, as more distant island populations have rounder wings. This is interesting because all Azorean blackcaps are supposed to be sedentary, so the more

pointed wings in the Eastern group islands, closer to the continent, could indicate the occurrence of some regular movements.

In any case, trends of size and shape change with different physical characteristics of the island are not well defined (low correlation values), especially for island area, and differences in morphology among island groups are rarely significant, except for birds from the islands of Corvo and Flores (which had relatively exaggerated size and shape patterns). And since the methodology was not directly oriented towards gathering information on drivers of ecomorphological change, it is not possible at the moment to take any conclusions regarding this topic.

There is however much work to be done in order to better understand the relationships between the insular environment and the patterns of morphological change in the Macaronesian Blackcap populations. Future work should include a larger sample, to enable a better characterization of each island's population, the origin of continental populations should as defined as possible and more extensive biometric characterization should be made. Focus should also be placed in trying to identify the ecological and physiological drivers of change in insular Blackcaps, to see to what extent the predictions of the island rule model explain the observed patterns.

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